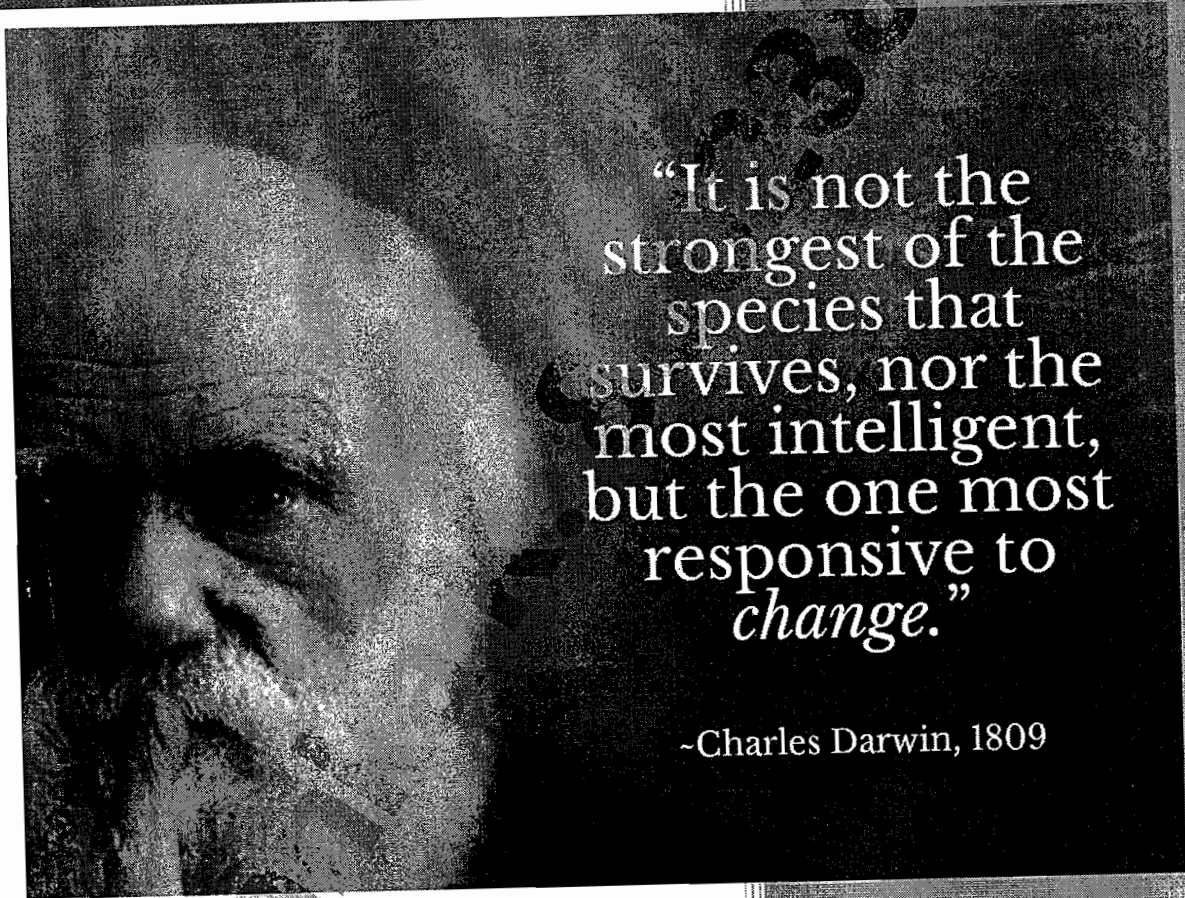


e|volution

2017

BOTANY: Evolutionary Biology



“It is not the
strongest of the
species that
survives, nor the
most intelligent,
but the one most
responsive to
change.”

~Charles Darwin, 1809

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0. Prescribed syllabus

Organic evolution – evidences, mechanism and theories

Role of RNA in origin and evolution of life

1. Organic evolution – evidences, mechanism and theories

The concept of organic evolution

The theory of evolution is one of the fundamental keystones of modern biological theory. It postulates that the various types of plants, animals, and other living things on Earth have their origin in other preexisting types and that the distinguishable differences are due to modifications in successive generations.

More than 2 million existing species of organisms have been named and described; many more remain to be discovered—from 10 million to 30 million, according to some estimates. The virtually infinite variations on life are the fruit of the evolutionary process. All living creatures are related by descent from common ancestors. Humans and other mammals descend from shrewlike creatures that lived more than 150 million years ago; mammals, birds, reptiles, amphibians, and fishes share as ancestors aquatic worms that lived 600 million years ago; and all plants and animals derive from bacteria-like microorganisms that originated more than 3 billion years ago.

Biological evolution is a process of descent with modification. Lineages of organisms change through generations; diversity arises because the lineages that descend from common ancestors diverge through time.

Evidences of organic evolution

The wide range of evidence of common descent of living things strongly indicates the occurrence of evolution and provides a wealth of information on the natural processes by which the variety of life on Earth developed, supporting the modern evolutionary synthesis.

Fossils are important for estimating when various lineages developed. As fossilization is an uncommon occurrence, usually requiring hard body parts and death near a site where sediments are being deposited, the fossil record only provides sparse and intermittent information about the evolution of life. Evidence of organisms prior to the

development of hard body parts such as shells, bones and teeth is especially scarce, but exists in the form of ancient microfossils, as well as impressions of various soft-bodied organisms.

Comparison of the genetic sequence of organisms has revealed that organisms that are phylogenetically close have a higher degree of sequence similarity than organisms that are phylogenetically distant. Further evidence for common descent comes from genetic detritus such as pseudogenes, regions of DNA that are orthologous to a gene in a related organism, but are no longer active and appear to be undergoing a steady process of degeneration. Since metabolic processes do not leave fossils, research into the evolution of the basic cellular processes is done largely by comparison of existing organisms. Many lineages diverged at different stages of development, so it is possible to determine when certain metabolic processes appeared by comparing the traits of the descendants of a common ancestor.

Evidence from paleontology

The remains or traces of organisms from a past geologic age embedded in rocks by natural processes are called fossils. They are extremely important for understanding the evolutionary history of life on Earth, as they provide direct evidence of evolution and detailed information on the ancestry of organisms. Paleontology is the study of past life based on fossil records and their relations to different geologic time periods.

For fossilization to take place, the traces and remains of organisms must be quickly buried so that weathering and decomposition do not occur. Skeletal structures or other hard parts of the organisms are the most commonly occurring form of fossilized remains. There are also some trace "fossils" showing moulds, cast or imprints of some previous organisms.

As an animal dies, the organic materials gradually decay, such that the bones become porous. If the animal is subsequently buried in mud, mineral salts will infiltrate into the bones and gradually fill up the pores. The bones will harden into stones and be preserved as fossils. This process is known as petrification. If dead animals are covered by wind-blown sand, and if the sand is subsequently turned into mud by heavy rain or floods, the same process of mineral infiltration may occur. Apart from petrification, the dead bodies of organisms may be well preserved in ice, in hardened resin of coniferous trees (amber), in tar, or in anaerobic, acidic peat. Fossilization can sometimes be a trace, an impression of a form. Examples include leaves and footprints, the fossils of which are made in layers that then harden.

Fossil records

Fossil trilobite. Trilobites were hard-shelled arthropods, related to living horseshoe crabs and spiders. That first appeared in significant numbers around 540 million years ago, dying out 250 million years ago.

It is possible to find out how a particular group of organisms evolved by arranging its fossil records in a chronological sequence. Such a sequence can be determined because fossils are mainly found in sedimentary rock. Sedimentary rock is formed by layers of silt or mud on top of each other; thus, the resulting rock contains a series of horizontal layers, or strata. Each layer contains fossils which are typical for a specific time period during which they were made. The lowest strata contain the oldest rock and the earliest fossils, while the highest strata contain the youngest rock and more recent fossils.

A succession of animals and plants can also be seen from fossil records. By studying the number and complexity of different fossils at different stratigraphic levels, it has been shown that older fossil-bearing rocks contain fewer types of fossilized organisms, and they all have a simpler structure, whereas younger rocks contain a greater variety of fossils, often with increasingly complex structures.

In the past, geologists could only roughly estimate the ages of various strata and the fossils found. They did so, for instance, by estimating the time for the formation of sedimentary rock layer by layer. Today, by measuring the proportions of radioactive and stable elements in a given rock, the ages of fossils can be more precisely dated by scientists. This technique is known as radiometric dating.

Throughout the fossil record, many species that appear at an early stratigraphic level disappear at a later level. This is interpreted in evolutionary terms as indicating the times at which species originated and became extinct. Geographical regions and climatic conditions have varied throughout the Earth's history. Since organisms are adapted to particular environments, the constantly changing conditions favoured species which adapted to new environments through the mechanism of natural selection.

According to fossil records, some modern species of plants and animals are found to be almost identical to the species that lived in ancient geological ages. They are existing species of ancient lineages that have remained morphologically (and probably also physiologically) somewhat unchanged for a very long time. Consequently, they are called "living fossils" by laypeople. Examples of "living fossils" include the tuatara, the nautilus, the horseshoe crab, the coelacanth, the ginkgo, the Wollemi pine, and the metasequoia.

Extent of the Fossil Record

Cynognathus, a Eucynodont, one of a grouping of Therapsids ("mammal-like reptiles") that is ancestral to all modern mammals.

Despite the relative rarity of suitable conditions for fossilization, approximately 250,000 fossil species are known. The number of individual fossils this represents varies greatly from species to species, but many millions of fossils have been recovered: for instance, more than three million fossils from the last Ice Age have been recovered from the La Brea Tar Pits in Los Angeles. Many more fossils are still in the ground, in various geological formations known to contain a high fossil density, allowing estimates of the

total fossil content of the formation to be made. An example of this occurs in South Africa's Beaufort Formation (part of the Karoo Supergroup, which covers most of South Africa), which is rich in vertebrate fossils, including therapsids (reptile/mammal transitional forms). It has been estimated that this formation contains 800 billion vertebrate fossils.

Evolution of the horse

Evolution of the horse showing reconstruction of the fossil species obtained from successive rock strata. Due to an almost-complete fossil record found in North American sedimentary deposits from the early Eocene to the present, the horse provides one of the best examples of evolutionary history (phylogeny).

This evolutionary sequence starts with a small animal called *Hyracotherium* (commonly referred to as *Eohippus*) which lived in North America about 54 million years ago, then spread across to Europe and Asia. Fossil remains of *Hyracotherium* show it to have differed from the modern horse in three important respects: it was a small animal (the size of a fox), lightly built and adapted for running; the limbs were short and slender, and the feet elongated so that the digits were almost vertical, with four digits in the forelimbs and three digits in the hindlimbs; and the incisors were small, the molars having low crowns with rounded cusps covered in enamel.

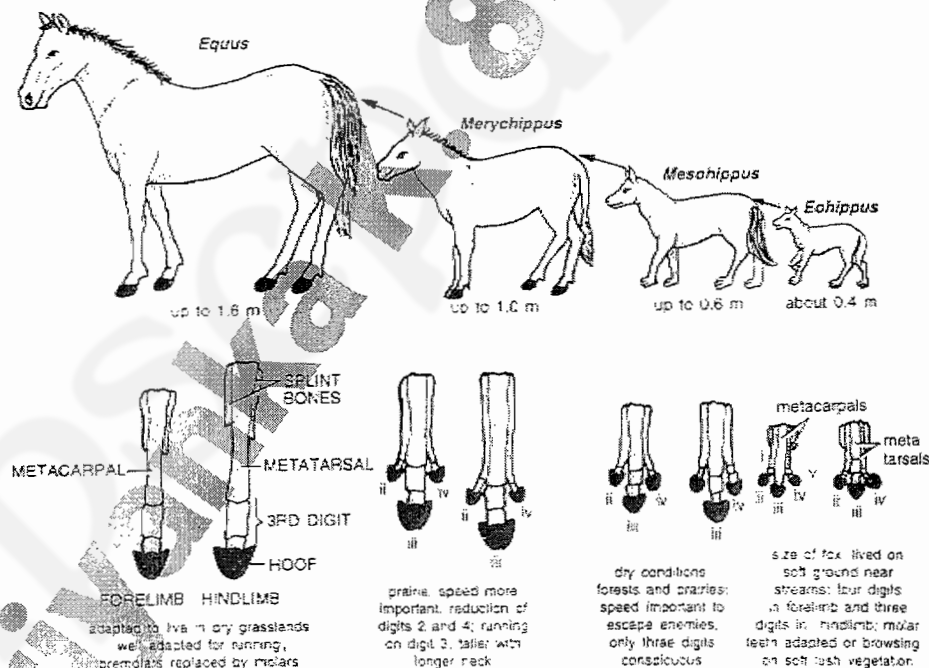


Figure 1: Phylogeny of horse.

The probable course of development of horses from *Hyracotherium* to *Equus* (the modern horse) involved at least 12 genera and several hundred species. The major trends seen in

the development of the horse to changing environmental conditions may be summarized as follows:

- Increase in size (from 0.4 m to 1.5 m);
- Lengthening of limbs and feet;
- Reduction of lateral digits;
- Increase in length and thickness of the third digit;
- Increase in width of incisors;
- Replacement of premolars by molars; and
- Increases in tooth length, crown height of molars.

Fossilized plants found in different strata show that the marshy, wooded country in which *Hyracotherium* lived became gradually drier. Survival now depended on the head being in an elevated position for gaining a good view of the surrounding countryside, and on a high turn of speed for escape from predators, hence the increase in size and the replacement of the splayed-out foot by the hooved foot. The drier, harder ground would make the original splayed-out foot unnecessary for support. The changes in the teeth can be explained by assuming that the diet changed from soft vegetation to grass.

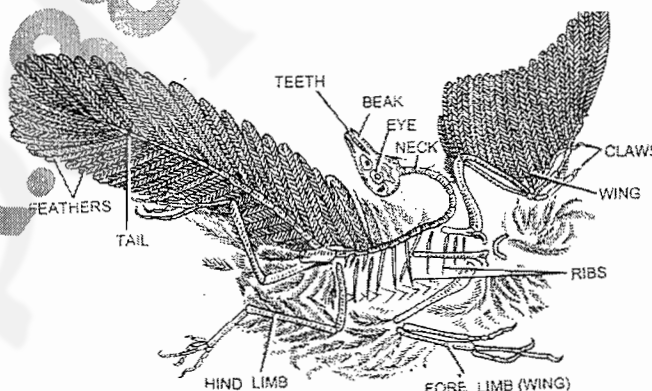
Limitations

The fossil record is an important source for scientists when tracing the evolutionary history of organisms. However, because of limitations inherent in the record, there are not fine scales of intermediate forms between related groups of species. This lack of continuous fossils in the record is a major limitation in tracing the descent of biological groups. Furthermore, there are also much larger gaps between major evolutionary lineages. When transitional fossils are found that show intermediate forms in what had previously been a gap in knowledge, they are often popularly referred to as "missing links".

There is a gap of about 100 million years between the early Cambrian period and the later Ordovician period. The early Cambrian period was the period from which numerous fossils of sponges, cnidarians, echinoderms, molluscs and arthropods are found. In the later Ordovician period, the first animal that really possessed the typical features of vertebrates, the Australian fish, *Arandaspis* appeared. Thus few, if any, fossils of an intermediate type between invertebrates and vertebrates have been found, although likely candidates include the Burgess Shale animal, *Pikaia gracilens*, and its Maotianshan shales relatives, *Myllokunmingia*, *Yunnanozoon*, *Haikouella lanceolata*, and *Haikouichthys*.

Some of the reasons for the incompleteness of fossil records are:

- In general, the probability that an organism becomes fossilized after death is very low;
- Some species or groups are less likely to become fossils because they are soft-bodied;
- Some species or groups are less likely to become fossils because they live (and die) in conditions that are not favourable for fossilization to occur in;
- Many fossils have been destroyed through erosion and tectonic movements;
- Some fossil remains are complete, but most are fragmentary;
- Some evolutionary change occurs in populations at the limits of a species' ecological range, and as these populations are likely to be small, the probability of fossilization is lower (see punctuated equilibrium);
- Similarly, when environmental conditions change, the population of a species is likely to be greatly reduced, such that any evolutionary change induced by these new conditions is less likely to be fossilized;
- Most fossils convey information about external form, but little about how the organism functioned;
- Using present-day biodiversity as a guide, this suggests that the fossils unearthed represent only a small fraction of the large number of species of organisms that lived in the past.



Missing Links

The transitional fossil forms which show characteristics of two different groups of living animals are called missing links. These are the fossil connecting links. Missing links are known between different existing groups from fishes to amphibians, from amphibians to reptiles and from reptiles to birds and mammals. With the help of missing links the evolutionary sequences of the major vertebrates can be represented.

The fossil connecting links are:

- Ichthyostega: It is a primitive fossil amphibian included in Stegocephalia (= Labyrinthodontia). Its fossils are obtained from late Devonian and Carboniferous

periods. It exhibits piscine as well as amphibian characteristics and is regarded as a connecting link between the two.

- **Seymouria:** It is a missing link between amphibians and reptiles. It was a lizard-like animal that lived about 250 million years ago. Its amphibian characters are short limbs, labyrinthine teeth and lateral line canals. The reptilian characters include two sacral vertebrae, an interclavicle and cleidoic eggs.
- **Archaeopteryx:** Six fossils of *Archaeopteryx* were obtained from upper Jurassic limestone rocks of Solenhofen in Bavaria, Germany. Its fossil is about 180 million years ago. It is missing link between reptile and birds.

Evidences from Embryology

These evidences are based on the comparative study of the embryos of various animals.

1. **Similarity in Early Development:** In all the multicellular animals the fertilized egg (zygote) undergoes segmentation (cleavage) to produce a solid structure, the morula. The morula develops into a single layered hollow blastula. The latter changes into either two or three layered gastrula. The animals having two layered gastrula are said to be diploblastic, e.g. coelenterates. The animals in which three layered gastrula is found are known as triploblastic, such as frog, lizard, etc. Diploblastic gastrula consists of ectoderm and endoderm. These two or three layers of gastrula are termed as primary germ layers, which give rise to the entire animal. Such a similar early development establishes a close relationship among all multicellular animals.
2. **Resemblance among Vertebrate Embryos:** If a comparative study of embryos of the same age of vertebrates, such as a fish, a salamander, a tortoise, a chick and a man is less the same form and structures like gill clefts, tail etc. although the embryos of all vertebrates resemble with one another but the embryos of closely related groups resemble more closely than the embryos of the distant groups. This is another evidence establishing close relationship among these divergent vertebrates.

Figure 2: *Archaeopteryx* fossil.

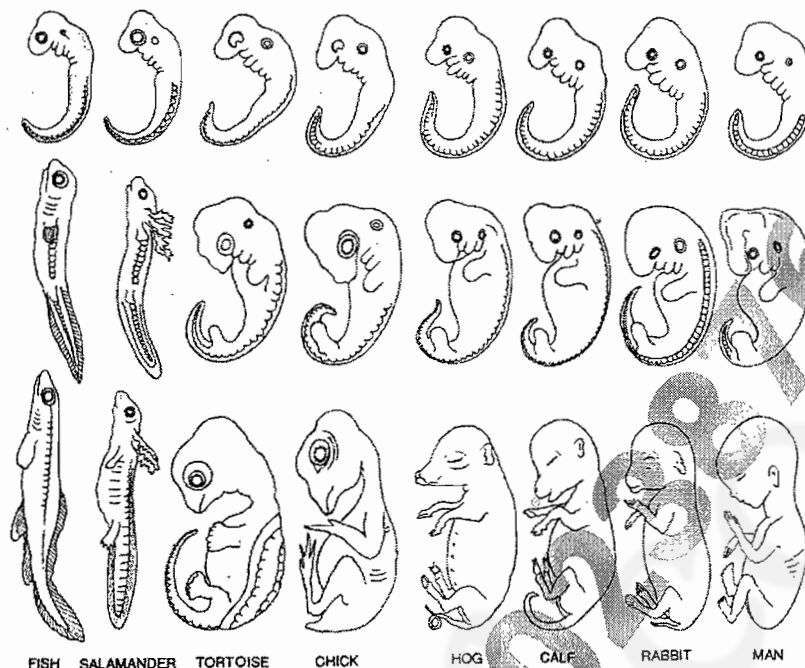


Figure 3: Remarkable similarity in the early embryos of some vertebrates.

3. **Resemblance among Invertebrate Larvae:** Annelids and molluscs possess a similar type of larva called trochophore. Echinoderms and hemichordates also have similar type of larva. Larvae resemblance points to a common ancestry.
4. **Progressive Metamorphosis:** Ammocoete larva of Lamprey resembles the adult form of *Amphioxus* or *Branchiostoma* in most of the details which are possible only if we presume that Lamprey has evolved from *Branchiostoma* like animals.
5. **Degenerate Organisms:** (Retrogressive Metamorphosis). Animals like *Sacculina* and tunicates (e.g. *Herdmania*) are degenerates and do not show any resemblance to other groups of animals. However, the study of their embryology has helped as to find their true systematic position on account of the characters presenting their embryos. *Sacculina* is a parasite on crabs. Limbs, mouth, alimentary canal and special sense organs are absent. The parasite has a stalked ovoid sac which sends outgrowths into the host for absorbing nourishment. The taxonomic position of *Sacculina* was found out through the study of its larva which resembles the nauplius larvae of crustaceans. Similarly, the tunicate *Herdmania* has simple purse like body which shows no trace to chordate connection. However, its larva possesses all the important chordate characteristics which proves that *Herdmania* is chordate.

6. **Temporary Embryonic Structure:** Embryos often possess structures which do not occur in the adults. For example, bird embryo has tooth buds and gill clefts which are not found in the adult animal. Presence of tooth buds has no relevance to the embryo as food is obtained from yolk through special blood vessels. The adult which feeds on hard grains and seed needs the teeth but is devoid of them. The presence of tooth buds in the embryos can be explained only on the assumption that (i) bird have developed from toothed ancestors; (ii) birds have lost teeth during evolution; (iii) the birds embryo possesses some ancestral characters due to the persistence of some genes that express their effect during development stages.

Whale is an aquatic mammal. It does not possess body hair. Its foetus or embryo possesses hair which are shed before birth. Hair are useless to the embryo because it is well protected inside the mother's body.

Early tadpole of frog possesses gills and tail, during metamorphosis these structures disappear.

7. **Development of Vertebrate organs:** Development of many vertebrate organs (e.g., heart, brain, and kidney) indicate the possible path of evolution as well as the common ancestry of vertebrates. For example, during its development the heart of a mammal or bird is initially two chambered then three chambered (as in amphibians and some reptiles) and ultimately four chambered. It clearly shows that birds and mammals have originated from fishes through and reptiles.

In all vertebrates, the brain arises as an anterior enlargement of the neural tube. Soon it develops two grooves and gets divided into three parts forebrain, midbrain and hindbrain. Each of these parts develops further to attain the adult state.

Vertebrates have three types of kidney pronephric, mesonephric and metanephric.. pronephric kidney occurs in hag fishes. Mesonephric kidneys is found in other fishes and amphibians while metanephric kidney is present in reptiles, birds and mammals. In the mammalian or bird embryo, the kidney is initially pronephric, then mesonephric and ultimately metanephric.

8. **Evidences from Plant embryos:** (a) In *Pinus* the foliage leaves do not occur directly on the main stems but are borne in clusters on the dwarf shoots. However, in seedling state the foliage leaves occur directly on the main stem indicating evolution *Pinus* from ancestors that possessed foliage leaves directly from ancestor that possess foliage leave directly on main stem. (b) Australian species of *Acacia* possess phyllodes or foliaceous petioles instead of normal bipinnate leaves as in other species of *Acacia*. Australian species show all the transitional steps between bipinnate leaves and phyllodes during the

seedling stage. (c) Many bryophytes pass through a filamentous protonema stage before attaining adult form. The filamentous protonema suggests algal ancestry for bryophytes. (d) Bryophytes and pteridophytes have ciliated male gametes or sperms. They require an external source of water for swimming to the female sex organs. In gymnosperms the sperms are transported by pollen tubes. Even then sperms of cycads and *Ginkgo* are ciliated.

9. **Recapitulation Theory/Biogenetic Law:** In 1828 Von Baer, the father of modern embryology proposed Baer's law which stated that during embryonic development the generalized features (such as brain, spinal cord, axial skeleton, aortic arches, etc. are common to all vertebrates) appeared earlier than the special features (like hair in mammals only features in birds only, limbs found in quadrupeds only) which distinguish the various members of the group. Later on this law was modified as the **biogenetic law** by **Ernst Haeckel** in 1866. Haeckel's biogenetic law states that "Ontogeny repeats phylogeny". Ontogeny is the life history of an organism while phylogeny is the evolutionary history of the race of that organism. In other words an organism repeats its ancestral history during its development.

Examples: (a) In the development of the frog a fish like tailed larva is formed, which swims with the tail and respites by gills this indicates that the frog has been evolved from a fish like ancestor.

(b) Tadpole (larva) of *Herdmania* shows characters of chordates i.e. presence of notochord, well developed dorsally placed central nervous system and tail, however, adult *Herdmania* does not have notochord and tail. Nervous system is also very much reduced in adult *Herdmania*. Thus the larva shows its ancestral characters.

(c) The protonema, an early stage in the development of a moss and a fern gametocyte resembles the filamentous green algae in structure, growth pattern and physiology. This indicates an algal ancestry of the bryophytes and pteridophytes.

(d) The gymnosperms have normally become independent of water in fertilization. But the primitive gymnosperms (e.g., *Cycas* and *Ginkgo*) have flagellated sperms and need water for fertilization like the pteridophyte. This indicates that the gymnosperms have descended from the pteridophyte like ancestor.

Evidence from comparative anatomy

Comparative study of the anatomy of groups of animals or plants reveals that certain structural features are basically similar. For example, the basic structure of all flowers

consists of sepals, petals, stigma, style and ovary; yet the size, colour, number of parts and specific structure are different for each individual species.

Homologous structures and divergent (adaptive) evolution

If widely separated groups of organisms are originated from a common ancestry, they are expected to have certain basic features in common. The degree of resemblance between two organisms should indicate how closely related they are in evolution:

- Groups with little in common are assumed to have diverged from a common ancestor much earlier in geological history than groups which have a lot in common;
- In deciding how closely related two animals are, a comparative anatomist looks for structures that are fundamentally similar, even though they may serve different functions in the adult. Such structures are described as homologous and suggest a common origin.
- In cases where the similar structures serve different functions in adults, it may be necessary to trace their origin and embryonic development. A similar developmental origin suggests they are the same structure, and thus likely to be derived from a common ancestor.

When a group of organisms share a homologous structure which is specialized to perform a variety of functions in order to adapt different environmental conditions and modes of life are called adaptive radiation. The gradual spreading of organisms with adaptive radiation is known as divergent evolution.

Brain Structure

Ranging from fishes to mammals, the brain consists of similar series of parts-olfactory lobes, cerebral hemispheres, optic lobes, cerebellum and medulla oblongata. As we progress through the series from fishes to mammals, some lobes present gradual enlargement (cerebral hemispheres). In fishes, the cerebral hemispheres are even smaller than the optic lobes, but in mammals they are so much enlarged that they cover the olfactory lobes in front and the optic lobes behind.

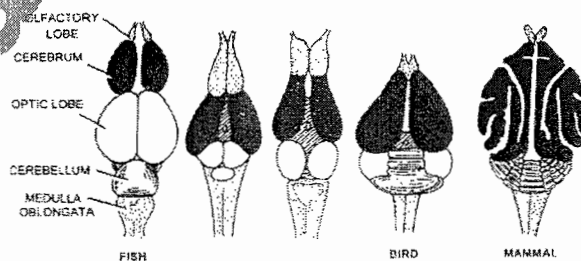


Figure 4: Homology in the parts of brain in fish, amphibia, reptile, birds and mammal.

Pentadactyl limb

The pattern of limb bones called pentadactyl limb is an example of homologous structures. It is found in all classes of tetrapods (*i.e.* from amphibians to mammals). It can even be traced back to the fins of certain fossil fishes from which the first amphibians are thought to have evolved. The limb has a single proximal bone (humerus), two distal bones (radius and ulna), a series of carpals (wrist bones), followed by five series of metacarpals (palm bones) and phalanges (digits). Throughout the tetrapods, the fundamental structures of pentadactyl limbs are the same, indicating that they originated from a common ancestor. But in the course of evolution, these fundamental structures have been modified. They have become superficially different and unrelated structures to serve different functions in adaptation to different environments and modes of life. This phenomenon is clearly shown in the forelimbs of mammals. For example:

- In the monkey, the forelimbs are much elongated to form a grasping hand for climbing and swinging among trees.
- In the pig, the first digit is lost, and the second and fifth digits are reduced. The remaining two digits are longer and stouter than the rest and bear a hoof for supporting the body.
- In the horse, the forelimbs are adapted for support and running by great elongation of the third digit bearing a hoof.
- The mole has a pair of short, spade-like forelimbs for burrowing.
- The anteater uses its enlarged third digit for tearing down ant hills and termite nests.
- In the whale, the forelimbs become flippers for steering and maintaining equilibrium during swimming.
- In the bat, the forelimbs have turned into wings for flying by great elongation of four digits, while the hook-like first digit remains free for hanging from trees.

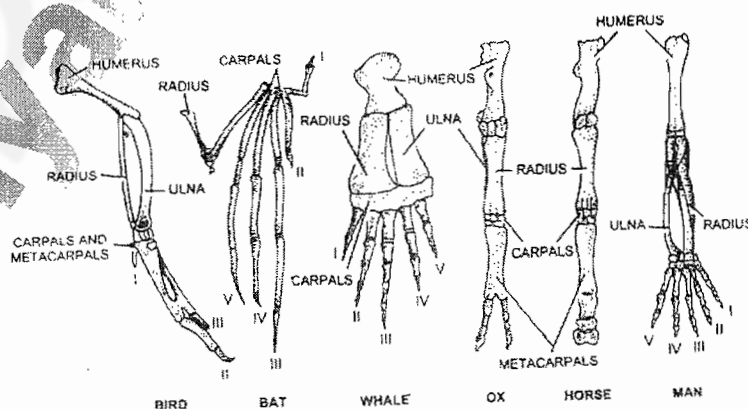


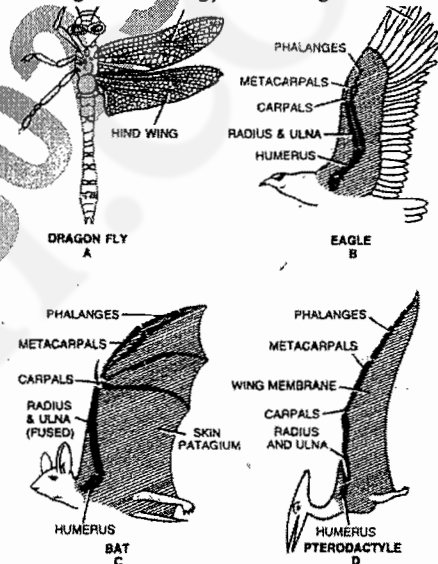
Figure 5: Homology in the forelimb of some vertebrates.

Insect mouthparts

The basic structures are the same, including a labrum (upper lip), a pair of mandibles, a hypopharynx (floor of mouth), a pair of maxillae, and a labium. These structures are enlarged and modified; others are reduced and lost. The modifications enable the insects to exploit a variety of food materials:

1. Primitive state — biting and chewing: *e.g.* grasshopper. Strong mandibles and maxillae for manipulating food.
2. Ticking and biting: *e.g.* honey bee. Labium long to lap up nectar; mandibles chew pollen and mould wax.
3. Piercing and sucking, *e.g.* female mosquito. Labrum and maxillae form tube; mandibles form piercing stylets; labrum grooved to hold other parts.
4. Sucking: *e.g.* butterfly. Labrum reduced; mandibles lost; maxillae long forming sucking tube.

Figure 6: Analogy in the wings.



Other arthropod appendages

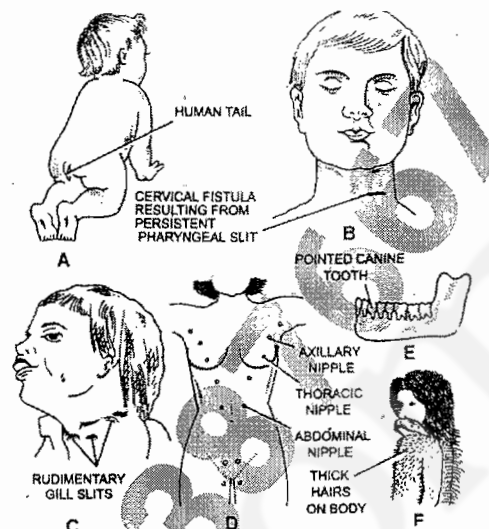
Insect mouthparts and antennae are considered homologues of insect legs. Parallel developments are seen in some arachnids: The anterior pair of legs may be modified as analogues of antennae, particularly in whip scorpions, which walk on six legs. These developments provide support for the theory that complex modifications often arise by duplication of components, with the duplicates modified in different directions.

Analogous structures and convergent evolution

Under similar environmental conditions, fundamentally different structures in different groups of organisms may undergo modifications to serve similar functions. This phenomenon is called convergent evolution. Similar structures, physiological processes or mode of life in organisms apparently bearing no close phylogenetic links but showing adaptations to perform the same functions are described as analogous, for example:

- Wings of bats, birds and insects;
- the jointed legs of insects and vertebrates;

- tail fin of fish, whale and lobster;
- eyes of the vertebrates and cephalopod molluscs (squid and octopus). Vertebrate eye has inverted retina and the sensory cells lying beneath the nerve fibres. This results in the sensory cells being absent where the optic nerve is attached to the eye, thus creating a blind spot. The octopus eye has a non-inverted retina in which the sensory cells lie above the nerve fibres. There is therefore no blind spot in this kind of eye. Apart from this difference the two eyes are remarkably similar, an example of convergent evolution.



Vestigial structures

A further aspect of comparative anatomy is the presence of vestigial organs. Organs that are smaller and simpler in structure than corresponding parts in the ancestral species are called vestigial organs. They are usually degenerated or underdeveloped. The existence of vestigial organs can be explained in terms of changes in the environment or modes of life of the species. Those organs are thought to be functional in the ancestral species but have now become unnecessary and non-functional. Examples are the vestigial hind limbs of whales, the haltere (vestigial hind wings) of flies and mosquitos, vestigial wings of flightless birds such as ostriches, and the vestigial leaves of some xerophytes (e.g. cactus) and parasitic plants (e.g. dodder). It must be noted, however, that vestigial structures have lost the original function but may have another one. For example the halteres in dipterists help balance the insect while in flight and the wings of ostriches are used in mating rituals.

Atavism or Reversion

Atavism or reversion is the reappearance of those ancestral characteristics in an organism or in the organisms of a group, which do not occur normally or which represent the reminiscent of normal structures possessed by the individuals of other groups.

Such abnormal structures are known as atavistic characters. There are several examples of reversion or atavism in man and other animals. In such cases abnormal characters or structures appear in the embryo or in the adult, which were not present either in the parent or grandparents but were found in some remote ancestors.

Evidence from geographical distribution

Data about the presence or absence of species on various continents and islands (biogeography) can provide evidence of common descent and shed light on patterns of speciation.

Figure 7: Atavism in the human body.

Continental distribution

All organisms are adapted to their environment to a greater or lesser extent. If the abiotic and biotic factors within a habitat are capable of supporting a particular species in one geographic area, then one might assume that the same species would be found in a similar habitat in a similar geographic area, e.g. in Africa and South America. This is not the case. Plant and animal species are discontinuously distributed throughout the world:

- Africa has short-tailed (Old World) monkeys, elephants, lions and giraffes.
- South America has long-tailed monkeys, cougars, jaguars and llamas.

Even greater differences can be found if Australia is taken into consideration, though it occupies the same latitude as much of South America and Africa. Marsupials like the kangaroo, the wallaby, and the wombat make up over 80 percent of Australia's indigenous mammal population. By contrast, marsupials are totally absent from Africa and are only represented by the opossum in South America and the Virginia Opossum in North America:

- The echidna and platypus, the only living representatives of primitive egg-laying mammals (monotremes), can be found only in Australia and are totally absent in the rest of the world.
- On the other hand, Australia has very few placental mammals and most of these either migrated from elsewhere (e.g. bats) or were introduced by human beings (e.g. rabbits).

Explanation

The main groups of modern mammal arose in Northern Hemisphere and subsequently migrated to three major directions:

- to South America via the land bridge in the Bering Strait and Isthmus of Panama; A large number of families of South American marsupials became extinct as a result of competition with these North American counterparts.
- to Africa via the Strait of Gibraltar; and
- to Australia via South East Asia to which it was at one time connected by land

The shallowness of the Bering Strait would have made the passage of animals between two northern continents a relatively easy matter, and it explains the present-day similarity of the two faunas. But once they had got down into the southern continents, they presumably became isolated from each other by various types of barriers.

- The submersion of the Isthmus of Panama: isolates the South American fauna.
- The Mediterranean Sea and the North African desert: partially isolate the African fauna.
- The submersion of the original connection between Australia and South East Asia: isolates the Australian fauna.

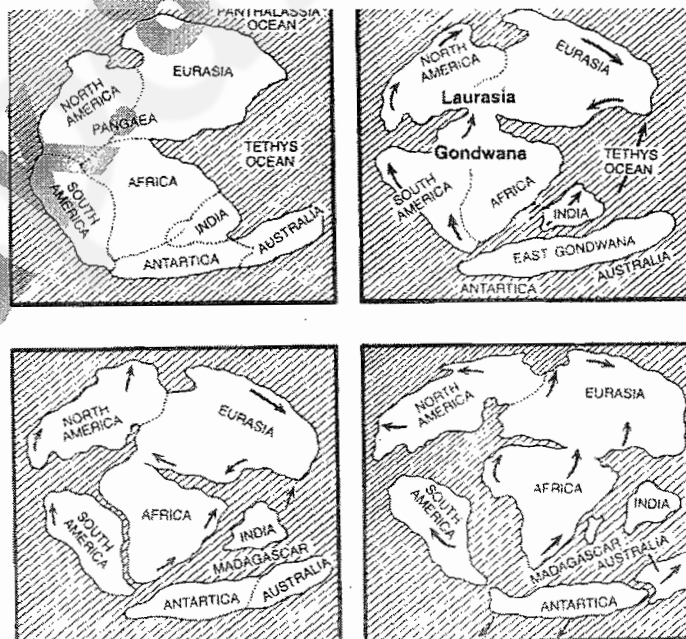
Once isolated, the animals in each continent have shown adaptive radiation to evolve along their own lines.

Evidence for migration and isolation

Map of the world showing distribution of present members of camel. Solid black lines indicate possible migration routes.

The fossil record for the camel indicated that evolution of camels started in North America, from which they migrated across the Bering Strait into Asia and hence to Africa, and through the Isthmus of Panama into South America. Once isolated, they evolved along their own lines, giving the modern camel in Asia and Africa and llama in South America.

Figure 8: Continental drift.



Continental drift

The same kinds of fossils are found from areas known to be adjacent to one another in the past but which, through the process of continental drift, are now in widely divergent geographic locations. For example, fossils of the same types of ancient amphibians, arthropods and ferns are found in South America, Africa, India, Australia and Antarctica, which can be dated to the Paleozoic Era, at which time these regions were united as a single landmass called Gondwana. Sometimes the descendants of these organisms can be identified and show

unmistakable similarity to each other, even though they now inhabit very different regions and climates.

Oceanic island distribution

Most small isolated islands only have native species that could have arrived by air or water; like birds, insects and turtles. The few large mammals present today were brought by human settlers in boats. Plant life on remote and recent volcanic islands like Hawaii could have arrived as airborne spores or as seeds in the droppings of birds. After the explosion of Krakatoa a century ago and the emergence of a steaming, lifeless remnant island called Anak Krakatoa (child of Krakatoa), plants arrived within months and within a year there were moths and spiders that had arrived by air. The island is now ecologically hard to distinguish from those around it that have been there for millions of years.

Evidences from Taxonomy

Classification of living organisms started as an artificial system and gradually it developed into a natural system based upon natural affinities and actual kinship (based on genetic relationship) found in the organism. It was devised by Linnaeus. It is, therefore, concluded that resemblances in animals are because these have arisen from a common stock, and differences in them are chiefly due to adaptation to different types of environments. All the animal phyla when viewed together seem to have relationship with one another but it is possible to arrange them in a series of increasing complexity on a ladder like diagram. It is easy to concede that protozoan come at the bottom and chordates at the top of ladder.

Taxonomists have summarized their studies in the form of tree like diagram in which phyla represent major branches of the tree of life. These are divided into several small branches, classes, which are divided into orders. This taxonomic tree with its branching system like a real tree represents an inter relationship among groups of organism descended from a common ancestor and modified along different lines. The living animals constitute the terminal twigs of the phylogenetic tree and do not exhibit any direct relationship. The fundamental relationship lies in the main branches and the trunk and the connecting links either exist as remote ancestors persisting today or die out in past and may be represented by fossils.

The mere fact that animals could be graded in order of increasing complexity is an evident of evolution. The natural system of classification is based upon similarity and such similarities of structures could be only due to origin from common ancestors.

Evidence from comparative physiology and biochemistry

Universal biochemical organisation

All known extant organisms are based on the same fundamental biochemical organisation: genetic information encoded as nucleic acid (DNA, or RNA for viruses), transcribed into RNA, then translated into proteins (that is, polymers of amino acids) by highly conserved ribosomes. Perhaps most tellingly, the Genetic Code is the same for almost every organism, meaning that a piece of DNA in a bacterium codes for the same amino acid as in a human cell. ATP is used as energy currency by all extant life.

Molecular variance patterns

A classic example of biochemical evidence for evolution is the variance of the protein Cytochrome c in living cells. The variance of cytochrome c of different organisms is measured in the number of differing amino acids, each differing amino acid being a result of a base pair substitution, a mutation. If each differing amino acid is assumed to be the result of one base pair substitution, it can be calculated how long ago the two species diverged by multiplying the number of base pair substitutions by the estimated time it takes for a substituted base pair of the cytochrome c gene to be successfully passed on. For example, if the average time it takes for a base pair of the cytochrome c gene to mutate is N years, the number of amino acids making up the cytochrome c protein in monkeys differ by one from that of humans, this leads to the conclusion that the two species diverged N years ago.

Comparison of the DNA sequences allows organisms to be grouped by sequence similarity, and the resulting phylogenetic trees are typically congruent with traditional taxonomy, and are often used to strengthen or correct taxonomic classifications. Sequence comparison is considered a measure robust enough to be used to correct erroneous assumptions in the phylogenetic tree in instances where other evidence is scarce. For example, neutral human DNA sequences are approximately 1.2% divergent (based on substitutions) from those of their nearest genetic relative, the chimpanzee, 1.6% from gorillas, and 6.6% from baboons. Genetic sequence evidence thus allows inference and quantification of genetic relatedness between humans and other apes. The sequence of the 16S ribosomal RNA gene, a vital gene encoding a part of the ribosome, was used to find the broad phylogenetic relationships between all extant life. The analysis, originally done by Carl Woese, resulted in the three-domain system, arguing for two major splits in the early evolution of life. The first split led to modern Bacteria and the subsequent split led to modern Archaea and Eukaryote.

The proteomic evidence also supports the universal ancestry of life. Vital proteins, such as the ribosome, DNA polymerase, and RNA polymerase, are found in everything from the most primitive bacteria to the most complex mammals. The core part of the protein is conserved across all lineages of life, serving similar functions. Higher organisms have evolved additional protein subunits, largely affecting the regulation and protein-protein

interaction of the core. Other overarching similarities between all lineages of extant organisms, such as DNA, RNA, amino acids, and the lipid bilayer, give support to the theory of common descent. The chirality of DNA, RNA, and amino acids is conserved across all known life. As there is no functional advantage to right- or left-handed molecular chirality, the simplest hypothesis is that the choice was made randomly by early organisms and passed on to all extant life through common descent. Further evidence for reconstructing ancestral lineages comes from junk DNA such as pseudogenes, "dead" genes which steadily accumulate mutations.^[4]

There is also a large body of molecular evidence for a number of different mechanisms for large evolutionary changes, among them: genome and gene duplication, which facilitates rapid evolution by providing substantial quantities of genetic material under weak or no selective constraints; horizontal gene transfer, the process of transferring genetic material to another cell that is not an organism's offspring, allowing for species to acquire beneficial genes from each other; and recombination, capable of reassorting large numbers of different alleles and of establishing reproductive isolation. The Endosymbiotic theory explains the origin of mitochondria and plastids (e.g. chloroplasts), which are organelles of eukaryotic cells, as the incorporation of an ancient prokaryotic cell into ancient eukaryotic cell. Rather than evolving eukaryotic organelles slowly, this theory offers a mechanism for a sudden evolutionary leap by incorporating the genetic material and biochemical composition of a separate species. Evidence supporting this mechanism has recently been found in the protist *Hatena*: as a predator it engulfs a green algae cell, which subsequently behaves as an endosymbiont, nourishing *Hatena*, which in turn loses its feeding apparatus and behaves as an autotroph.

Since metabolic processes do not leave fossils, research into the evolution of the basic cellular processes is done largely by comparison of existing organisms. Many lineages diverged when new metabolic processes appeared, and it is theoretically possible to determine when certain metabolic processes appeared by comparing the traits of the descendants of a common ancestor or by detecting their physical manifestations. As an example, the appearance of oxygen in the earth's atmosphere is linked to the evolution of photosynthesis.

Out of Africa hypothesis of human evolution

Mathematical models of evolution, pioneered by the likes of Sewall Wright, Ronald Fisher and J. B. S. Haldane and extended via diffusion theory by Motoo Kimura, allow predictions about the genetic structure of evolving populations. Direct examination of the genetic structure of modern populations via DNA sequencing has recently allowed verification of many of these predictions. For example, the Out of Africa theory of human origins, which states that modern humans developed in Africa and a small sub-population migrated out (undergoing a population bottleneck), implies that modern populations should show the signatures of this migration pattern. Specifically, post-bottleneck populations (Europeans and Asians) should show lower overall genetic

diversity and a more uniform distribution of allele frequencies compared to the African population. Both of these predictions are borne out by actual data from a number of studies.

Evidence from genetics

Although it has only recently become available, the best evidence for common descent comes from the study of gene sequences. **Comparative sequence analysis** examines the relationship between the DNA sequences of different species, producing several lines of evidence that confirm Darwin's original hypothesis of common descent. If the hypothesis of common descent is true, then species that share a common ancestor will have inherited that ancestor's DNA sequence. Notably they will have inherited mutations unique to that ancestor. More closely-related species will have a greater fraction of identical sequence and will have shared substitutions when compared to more distantly-related species.

The simplest and most powerful evidence is provided by **phylogenetic reconstruction**. Such reconstructions, especially when done using slowly-evolving protein sequences, are often quite robust and can be used to reconstruct a great deal of the evolutionary history of modern organisms (and even in some instances such as the recovered gene sequences of mammoths, Neanderthals or *T. rex*, the evolutionary history of extinct organisms). These reconstructed phylogenies recapitulate the relationships established through morphological and biochemical studies. The most detailed reconstructions have been performed on the basis of the mitochondrial genomes shared by all eukaryotic organisms, which are short and easy to sequence; the broadest reconstructions have been performed either using the sequences of a few very ancient proteins or by using ribosomal RNA sequence.

This evidence does not support the rival hypothesis that genetic similarity of two species is the product of common functional or structural requirements, and not common descent (for example, if there is one best way to produce a hoof, all hoofed creatures will share a genetic basis even if they are not related). However, phylogenetic relationships also extend to a wide variety of non-functional sequence elements, including repeats, transposons, pseudogenes, and mutations in protein-coding sequences that do not result in changes in amino-acid sequence. While a minority of these elements might later be found to harbor function, in aggregate they demonstrate that identity must be the product of common descent rather than common function.

Finally, a deeper understanding of developmental biology shows that common morphology is, in fact, the product of shared genetic elements. For example, although camera-like eyes are believed to have evolved independently on many separate occasions, they share a common set of light-sensing proteins (opsins), suggesting a common point of origin for all sighted creatures. Another noteworthy example is the familiar vertebrate body plan, whose structure is controlled by the homeobox (Hox) family of genes.

Evidence from speciation

Hawthorn fly: One example of evolution at work is the case of the hawthorn fly, *Rhagoletis pomonella*, also known as the apple maggot fly, which appears to be undergoing sympatric speciation. Different populations of hawthorn fly feed on different fruits. A distinct population emerged in North America in the 19th century some time after apples, a non-native species, were introduced. This apple-feeding population normally feeds only on apples and not on the historically preferred fruit of hawthorns. The current hawthorn feeding population does not normally feed on apples. Some evidence, such as the fact that six out of thirteen allozyme loci are different, that hawthorn flies mature later in the season and take longer to mature than apple flies; and that there is little evidence of interbreeding (researchers have documented a 4-6% hybridization rate) suggests that this is occurring. The emergence of the new hawthorn fly is an example of evolution in progress.

Evidence from antibiotic and pesticide resistance

The development and spread of antibiotic resistant bacteria, like the spread of pesticide resistant forms of plants and insects is evidence for evolution of species, and of change within species. Thus the appearance of vancomycin resistant *Staphylococcus aureus*, and the danger it poses to hospital patients is a direct result of evolution through natural selection. The rise of *Shigella* strains resistant to the synthetic antibiotic class of sulfonamides also demonstrates the generation of new information as an evolutionary process. Similarly, the appearance of DDT resistance in various forms of *Anopheles* mosquitoes, and the appearance of myxomatosis resistance in breeding rabbit populations in Australia, are all evidence of the existence of evolution in situations of evolutionary selection pressure in species in which generations occur rapidly.

Evolutionary mechanisms

Sequential and divergent evolution

Evolution is the process of gradual modification in the living organisms so as to establish diversity in the world of living beings. Two fundamental patterns could be envisaged in the process of evolution:

1. Minor changes in the gene pool of a population are passed on from one generation to the next, with the result that no new populations are formed, but the descendent population is not genetically identical with its predecessor. This is known as **sequential evolution**.
2. The changes which result in sudden evolution of new populations, species, families, groups or classes represent as **divergent evolution**.

Sequential evolution.

The sequential evolution is, therefore, an example of random fluctuations over a long period of time without producing new populations. Therefore, the changes occurring, on account of evolutionary forces like mutations, variations, natural selection and genetic drifts produce only temporary changes which fluctuate at random. For example, in human population, we find that not even two real sisters or brothers are identical or resemble their parents, yet the changes do not divide the individuals of a population or race into subcategories. Secondly, these changes are not directional.

Divergent evolution.

The divergent evolution, on the contrary, is an example of directional evolution. The changes occur in a cumulative direction and result in the origin of new populations from the old ones. Therefore, the varied groups of plants and animals either related or unrelated provide an example of divergent evolution. It is the divergent evolution which is more evident.

As a matter of fact the two aspects are rather inseparable. Not even a single population exclusively exhibits sequential evolution, because all populations diverge in due course of time and split up into new populations. Moreover, the forces responsible for bringing about changes are rather the same in both the cases except that they operate for a very long period and are assisted by additional factors.

Sequential evolution though helps in understanding the operation of various evolutionary forces, does not play any role in the evolution of new species or groups. It is, therefore, the divergent evolution which is seen in fossil records and which actually illustrates the phenomenon of evolution.

Micro, Macro and Mega-evolution

Goldschmidt has divided evolution into 2 categories:

1. **Microevolution:** Evolution of subspecies or geographic races. The sequential evolution is actually microevolution and the divergent evolution in its simplest form *i.e.*, operating at the population level is also nothing but microevolution only.
2. **Macroevolution:** Evolution of species, genera and so on. Evolutionary changes which are responsible for establishing the taxonomic categories above species level represent macroevolution.

Megaevolution for the large scale evolution of families, orders, classes and phyla. Simpson In 1953 has added the term Megaevolution.

Microevolution

The evolution, *which results from the interaction of the elemental forces of evolution (i.e., mutation, variations, recombination, natural selection and the genetic drifts) to produce relatively small changes in the population or populations*, is known as microevolution. The basic process of microevolution consists of change in the gene frequencies in a population from one generation to the next. The microevolution, therefore, operates to change the genetic equilibrium in a Mendelian population and occurs below the species level.

Microevolutionary Forces: The "micromutations" or "little mutations" as described by Goldschmidt are the main source of producing changes in the gene frequencies in the gene pool of local populations. Genetic recombination or Mendelian recombination changes the gene frequency in the gene pool of the population. In addition, genetic drift and natural selection also operate on the population to change their gene frequency and thereby disturb the genetic equilibrium.

Mechanism of Microevolution: The genetic material of the living beings has tendency to change. The changes in the structure or composition of genes are described as gene mutations. These may be spontaneous or may be induced by certain chemicals and environmental factors like radiation, etc. The recombination of genes by interbreeding also helps in the introduction of new combinations of already existing genes and introduces variations. Interbreeding helps in the spread of micro-mutations.

The variations introduced in a gene pool of population by mutations and recombination are operated upon by the natural selection. As a result, the offsprings of population are found to be different genetically as well as phenotypically. This changed population or descent population is the product of microevolution.

Changes produced by mutation and recombination may be beneficial or may not be so. But since the changed genotype interacts with the environment, only those changes which increase the rate of reproduction of the organisms become more numerous in the population.

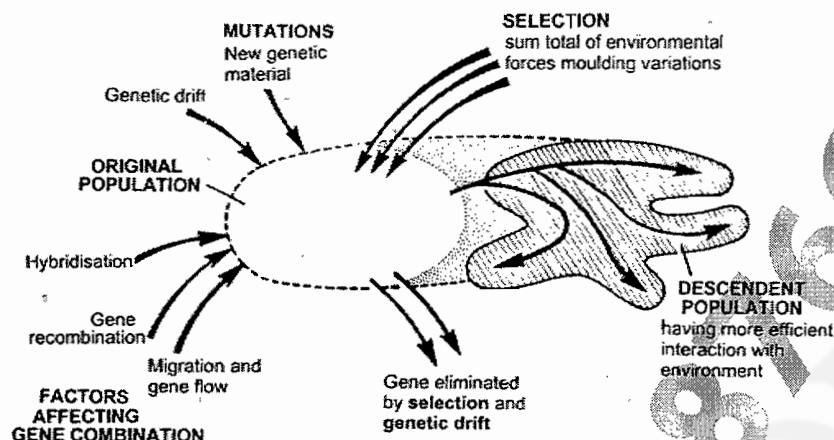


Figure 1: Mechanism of microevolution.

Microevolutionary forces operating for a shorter period produce sequential evolution, whereas when continued for generations together result in the evolution of new populations from the existing one. The origin of new populations can occur in two different ways:

1. In a successional manner, and
2. In a divergent manner.

The **successional microevolution** is the evolution within a single population which results in the successional replacement of the pre-existing populations by the new ones. This could be seen in successive strata of palaeontological series. It leads to microevolution to the formation of **clines**, when characters of a population seem to change gradually across its place of distribution. The formation of clines is an example of gradual changes in response to gradual changes in the climate.

The **divergent microevolution** results in the splitting of parental population into two or more new populations with the appearance of genetic divergence. Isolation is the additional factor operating to establish genetic divergence in the related populations.

Examples of Microevolution: A number of series of invertebrate fossils provide an example of microevolution. For example, Rowe has traced several lines of descent in the fossil genera of sea urchin, *Micraster*. In one of these series there is a gradual replacement of the *M. corbovis* by *M. coranguinum*. Another example of microevolution leading to the replacement of an old species by a new species is offered by *Spirifer*, a branchiopod.

The microevolution is, therefore, a continuous and gradual change in the interbreeding populations, which become geographically isolated into local populations. Then each one of these develops small variations, which gradually accumulate to produce large differences in their morphology or physiology, so that each such local population becomes markedly different from other and from the parent population. The variations

occur on account of micromutations and recombination and are favoured by natural selection.

Macroevolution (Adaptive Radiation)

The evolution, which results in the production of new adaptive types through a process of population fragmentation and genetic divergence, is known as macroevolution. It operates above the species level and results in the splitting of the population of a species into several subgroups, each of which exhibits changes in a definite adaptive direction. These changes are known as adaptive trends and the phenomenon as the adaptive radiation or macroevolution. It means macroevolution is actually adaptive radiation.

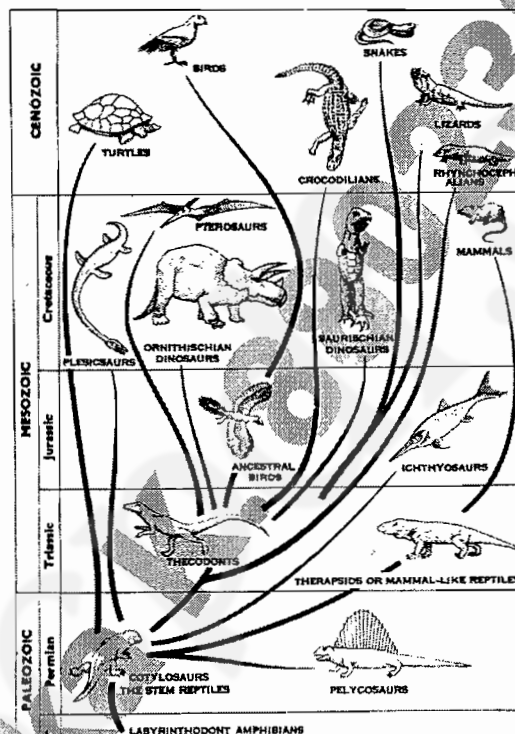


Figure 2: Adaptive radiation or macroevolution in reptiles.

Mechanism of Macroevolution: Macroevolution operates above species level and results in the establishment of new genera, families and orders. The changes in the organisation occur on account of sudden mutations of large size, which are named "macromutations" or "systematic mutations" by Goldschmidt. Macroevolution occurs in a group of individuals which have entered a new adaptive zone free of competition.

In a new adaptive zone, the number of individuals is far less and the opportunities to avail new habitats are more. Therefore, the intraspecific struggle is roughly nil. Moreover, the new zone will be almost free from the enemies. Thus, the newly entered population enters all the available habitats of the adaptive zone and starts adapting themselves according to the conditions and need. It means that the one population

which had acquired the new zone gets splitted-up into several subpopulations, each of which accumulates mutations and evolves independently but, simultaneously in different directions. On account of the different environmental conditions, adaptive modifications occur in different directions. Adaptive modifications in each subpopulation have a cumulative effect and are, therefore, directional.

Examples of Macroevolution: Evolution of reptiles and horse represents the best documented examples of macroevolution in the fossil records. Class Reptilia first appeared in the fossil records in Pennsylvanian Period. Adaptive radiation in the group occurred between Permian and Cretaceous Periods. The divergent evolution or adaptive radiation of different reptilian or amphibian groups from initial reptiles and amphibian ancestors are examples of macroevolution. These earliest reptiles were Cotylosaurs. All the living and fossil groups of reptiles have evolved from them. The evolution of reptiles actually represents six major radiating offshoots from the basal anapsid stock. These exhibit further diversification of their populations resulting in the formation of orders and then families and so on.

Evolution of Horse family, *Equidae* from *Hyracotherium* is another example of adaptive radiation or macroevolution. It exhibits gradual changes in the structure of teeth, limbs and hoof from a small dog-like browsing creature with padded feet to modern horse with the large size, grazing habits and hooved feet.

Essential Features of Macroevolution

1. Macroevolution occurs on account of macro-mutations.
2. Macroevolution occurs in those populations which have entered or acquired a new adaptive zone.
3. Macroevolution results in evolutionary divergence i.e., the pre-existing population divides into several diverging descendent populations by acquiring special adaptations.
4. Macroevolution produces groups of parallel special adaptations among divergent stocks.
5. Macroevolution leads to specialisation in a particular direction. As a result, forms with special adaptations become rigidly specialised to narrow adaptive subzones and reach the adaptive peak. This very often leads to overspecialisation and finally to the extinction because overspecialised forms are unable to modify when they enter a new adaptive zone.

Megaevolution

Megaevolution has been described as *the origin or evolution of new types of biological organisation, as a result of general adaptation from its predecessor, resulting in the formation of new classes, groups or phyla*. Megaevolutionary changes are rare and have occurred only a few times in the evolutionary history of living beings. But the most interesting thing is that all these biological organisations persist without extinction

(with few exceptions). All the phyla and most of the classes of micro-organisms, plants and animals represent their separate organisation and are produced as a result of megaevolution. The origin of amphibians from fishes, origin of reptiles from amphibians and the origin of birds and mammals from reptiles offer best examples of megaevolution.

Mechanism of Megaevolution: During megaevolution the organisms of the ancestral stock attempt to enter a new zone, which is uninhabited by these forms and is devoid of competition. These exhibit varied modifications in different directions until one of these is found suitable to the new zone. It means a group of individuals of the parental stock develops certain generalised preadaptations which enable them to enter the new zone. Therefore, these make a breakthrough into the new adaptive zone and start radiating into all the available habitats, thereby developing more specialised adaptations which are known as postadaptations.

The mechanism of megaevolution can be explained by taking origin of reptiles from amphibians as an example. Amphibians are amphibious creatures which could live in moist places near some source of water. Reptiles evolved as completely terrestrial forms which need not depend on aquatic medium at any stage of their life cycle. At that time the terrestrial zone was unoccupied, devoid of competition and accessible. The principal new general preadaptations which evolved in some of the ancestral amphibians and made the invasion of terrestrial zones are:

1. The development of exoskeleton in the form of scales, plates or scutes which prevented desiccation of the adults.
2. The appearance of large cleidoic eggs which enabled the young ones to develop on land.

Similarly, origin of birds from some primitive reptiles includes the sudden appearance of wings which enabled the ancestral form to make the invasion of aerial zone. The fossils of ancestral bird, *Archaeopteryx*, exhibit reptilian characteristics together with wings and feathers.

Evolution of mammals can be traced back to a series of fossil synapsid reptiles of the group Therapsida. These developed several mammalian characteristics like the false palate, teeth differentiated into incisors, canines, premolars and molars, and the limbs became modified so that the elbows and knees were placed under the body. But still these forms were reptiles because teeth were without roots and the quadrate and articular bones did not form the ossicles. In Therapsid group the main preadaptation towards mammalian offshoot was freeing of the quadrate and articular bones from jaw articulation and their conversion into ear ossicles. The particular change served two purposes: 1. It improved hearing, and 2. Direct articulation of mandible or dentary with the skull strengthened the jaws.

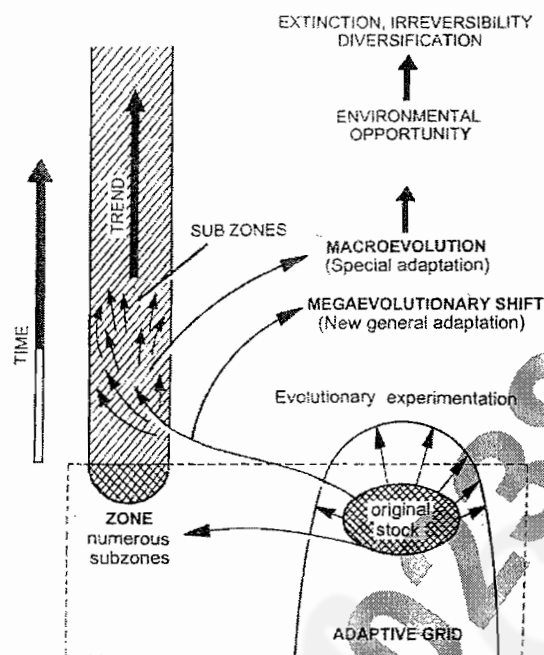


Figure 3: Mechanism of macro and megaevolution.

Special Features of Megaevolution

The fossil evidences in favour of megaevolution are relatively rare. The megaevolution, therefore, exhibits following special features:

1. Megaevolution includes experimentation and exploitation of new zone by the members of the ancestral stock in several divergent lines. This experimentation involves appearance of new characteristics which may prove suitable for a new zone.
2. Megaevolution operates on individuals which have developed some general adaptations for the new zone.
3. The preadapted group of individuals then crosses the ecological barriers and makes a breakthrough into the new zone.
4. The breakthrough and shifts are always rapid; otherwise they fail because of extreme negative selection in unstable ecological zone.
5. The new zone is always ecologically accessible and is devoid of competition.
6. The initial shift is always followed by adaptive radiation which is actually macroevolution.

Common Features of Macroevolution and Megaevolutions

Macroevolution and megaevolution are highly complex phenomena. These have following characteristics in common:

1. Taking one of the new adaptations for entering into new adaptive zone (**preadaptations**).
2. Invasion of the new zones or sub zones within the new adaptive zone by the development of special adaptations (**postadaptations**).
3. Loss of evolutionary flexibility and channelisation into greater and greater specialization for the ecological conditions of subzones.
4. Reinvasion of the zones and sub zones which become partially unoccupied on account of the specialisation of the original occupants.
5. Megaevolution is always followed by macroevolution.

The three levels of evolution i.e., the micro, macro and megaevolution differ to a considerable degree from one another but all are based upon microevolutionary process and all contribute to adaptations. The elemental forces for the three types of evolution are the same but macro and megaevolution have some additional forces. The microevolution may be sequential or divergent but the latter two are always divergent and involve adaptive radiation and divergence.

Theories of evolution

Four theories have been put forward to explain the mode of evolution.

1. Lamarckism or Lamarck's theory of the inheritance of acquired characters.
2. Darwinism or Darwin's theory of natural selection.
3. Hugo de Vries' mutation theory
4. Modern concept of evolution.

Lamarckism

Lamarckism is the first theory of evolution, which was proposed by **Jean Baptiste de Lamarck** (1744-1829), a French biologist. Although the outline of the theory was brought to notice in 1801, but his famous book "**Philosophic Zoologique**" was published in 1809, in which he discussed his theory in detail.

Lamarck's Propositions

Lamarckism includes four main propositions.

1. **Internal Vital Force.** All the living things and their component parts are continually increased due to internal vital force.
2. **Effect of Environment and New Needs.** Environment influences all types of organisms. A change in environment brings about changes in organisms. It gives rise to new needs. New needs or desires produce new structures and change habits of the organisms. Doctrine of desires is called **appetency**.
3. **Use and Disuse of Organs.** If an organ is constantly used it would be better developed whereas disuse of organ results in its degeneration.

4. **Inheritance of Acquired Characters.** Whatever an individual acquires characters in its life time due to internal vital force, effect of environment, new needs and use and disuse of organs, they are inherited (transmitted) to the next generations. The process continues. After several generations, the variations are accumulated up to such extent that they give rise to new species.

Examples in Support of Lamarckism

Lamarck explained his theory by giving the following examples.

1. **Evolution of Giraffe.** The ancestors of giraffe were bearing a small neck and forelimbs and were like horses. But as they were living in places with no surface vegetation, they had to stretch their neck and fore-limbs to take the leaves for food, which resulted in the slight elongation of these parts. Whatever they acquired in one generation was transmitted to the next generation with the result that a race of long necked and long fore-limbed animals was developed.
2. **Webbed Toes of Aquatic Birds.** Aquatic birds like ducks have been evolved from the terrestrial ancestors. Since they had to go to water due to lack of food, etc. some structures like web between the toes developed in them, so that they could live in water easily. The wings were not used for flying as they were not needed, and later on they got reduced.
3. **Disappearance of Limbs in Snakes.** The snakes have been evolved from lizard like ancestors which were having two pairs of limbs. These lizards like ancestors of snakes felt insecure from the mammals of that time, because the latter were more powerful and numerous in number. To escape from the mammals, the ancestors of the snakes started living in narrow holes or crevices and in thick jungles. To accommodate their body in narrow spaces they could not use their limbs, that is why the limbs were reduced and finally disappeared, while their body became longer and cylindrical.
4. **Flat Fishes.** They are flat and bear both the eyes on one side and live at the bottom of the water. During the embryonic stage their eyes are present laterally, one eye on either side. The bodies of these fishes is not flat at this stage but later on both the eyes are shifted to one side and the body becomes flat to withstand the pressure of water.
5. **Flightless Birds.** The ancestors of these birds (*e.g.*, Ostrich) were capable of flying, but due to some environmental factors they had plenty of food and were well protected. So they did not use their wings and that is why the latter became vestigial.
6. **Retractable Claws of Carnivorous Mammals.** The ancestors of carnivorous mammals such as lions, tiger etc. had ordinary claws for tearing the flesh of their preys. As the latter gained in running, the carnivorous mammals also had to run fast for which claws were a hindrance. The animals, therefore, developed retractile claws.
7. **Deer.** The ancestors of deer were not having so much speed in running, but as they needed protection from other animals of that time they started running, due

to which present speed was achieved by the deer and consequently their limbs got developed and the body became streamlined.

8. **Cave Dwellers.** The ancestors of cave dwellers had normal eye sight. On account of living under continuous dark conditions, the animal lost their power to see.
9. **Emergent Hydrophytes.** The effect of environment and inheritance of acquired characters is clearly seen in emergent hydrophytes like *Ranunculus aquatilis*. Here the submerged leaves are dissected while the emerged ones are simply lobed. When the plant is grown out of water, all the leaves are undissected. In the submerged environment all the leaves are dissected.

Criticism of Lamarckism

(Evidences against the Inheritance of Acquired Characters)

The first proposition of the theory does not have any ground because there is no vital force in organisms which increases their body parts. As regards the second proposition, the environment can affect the animal but it is doubtful that a new need forms new structures. The third proposition, the use and disuse of the organs is correct up to some extent. The fourth proposition regarding the inheritance of acquired characters is disputed.

Mendel's **Laws of Inheritance** and Weismann's **Theory of Continuity of Germplasm** (1892) discarded Lamarck's concept of inheritance of acquired characters.

Theory of Continuity of Germplasm

August Weismann (1834-1914), a German biologist, was the main opposer of the inheritance of acquired characters. He put forward the theory of continuity of germplasm. According to Weismann, the characters influencing the germ cells are only inherited. There is a continuity of germplasm (protoplasm of germ cells) but the somatoplasm (protoplasm of somatic cells) is not transmitted to the next generation hence it does not carry characters to next generation. Weismann cut off the tails of rats for as many as 22 generations and allowed them to breed, but tailless rats were never born.

Other examples. Boring of pinna (external ear) and nose of Indian women is never inherited to the next generations. The wrestler's powerful muscles are not transmitted to the offspring. European ladies wear tight waist garments in order to keep their waist slender but their offspring at the time of birth have normal waists. A similar example can be quoted from Chinese women. They used to wear iron shoes in order to have small feet, but their children at the time of birth have always normal feet. Circumcision of penis is in Jews and Muslims but it is not inherited to the next generation.

Evidences in favour of the Inheritance of Acquired Characters

1. In certain cases *somatic cells can produce the germ cells*, which is against Weismann's theory of continuity of germplasm. This occurs in vegetative propagation in plants and regeneration in animals.
2. **Harrison** found the occurrence of a dark variety of moth in localities having manganese pollution. He fed the natural pale variety of moth for several generations on manganese rich diet. It produced the dark or melanic variety which bred true. Harrison's observations indicate the *effect of environment on germ cells through somatic cells*.
3. **Tower** exposed the young developing Potato Beetles to extremes of temperature and humidity at the time of the development of their reproductive organs. This did not produce any change in the beetles themselves. Their offspring, however, had colour variations, which were passed on to the succeeding generations. Tower's observations indicate *direct effect of environment on germ cells*.
4. Exposure of organisms to high energy radiations (ultra-violet rays, X-rays, gamma rays, etc.) or feeding them with mutagenic chemicals, produces sudden inheritable variations or mutations. For example, **Auerbach et al** obtained a number of mutations and chromosome aberrations in *Drosophila* with the help of mustard gas.
5. **Agar** reared water fleas in a culture of green flagellates and found that some abnormalities were developed in their structures. The parthenogenetic eggs of such individuals when kept in ordinary water and allowed to hatch produced individuals with the same abnormalities.
6. There is no isolation of somatic and germ cells. Rather one part of the body affects other parts of the body through chemicals called hormones. Change in the secretion of hormones results in the change of different parts of the body.
7. **Guyar and Smith** took the solution of the eye lens of rabbit and inoculated the same into fowl. The fowl's serum containing antibodies was injected into pregnant rabbits. Some of the offspring were found to have malformed or degenerate eyes.
8. Radish is a two-year crop in cold countries but completes its growth in one year in tropical areas. Similarly, deciduous European Peach becomes evergreen in India.

Neo-Lamarckism

According to Neo-Lamarckism the acquired characters which become incorporated in the germplasm are heritable and accumulate generation after generation resulting the origin of new forms or new species. It was strongly advocated by **T. H. Morgan** and **Cope**.

Experiments in Support of Inheritance of Acquired Characters

The following examples support Neo-Lamarckism

1. **Bonner** carried out numerous transplantation experiments within native and unnatural environments and found that variation produced were inherited to their future generation.
2. The white mice which were reared at a high temperature were, found to develop a longer body, a longer tail and longer hindlimbs. This character was found to be transmitted to the offsprings generation after generation.
3. **Tower** exposed some potato beetles to abnormal conditions of temperature and humidity at a stage when their reproductive organs were developing. The offspring of these beetles showed colour variation and these were passed on to offsprings.
4. **Brown Squared** described that certain diseases like exophthalmia, haematoma and dry gangrene are caused by injuries in the restiform body of the brain and are inherited to the offsprings.
5. **Mc Doughall** trained rats to follow certain escape routes from a tank of water and the training was given for about 45—50 generations. It was found that there was a decrease in number of errors made in learning the problem generation after generation.
6. Cells exposed to X-rays or treated with certain chemical (like colchicines, mustard gas, etc.) cause changes in chromosome structure (chromosomal aberrations).

Neo- Lamarckian Explanation

Neo-Lamarckians explain the above observations as follows:

1. **Formation of Germ Cells from Somatic Cells:** In case of asexual reproduction and vegetative propagation, the germ cells are derived from the somatic cells. These have chromosomes and genes, similar to the parent. For example, plants raised from tubers, stem cutting or from leaf buds or underground stem inherit genes and chromosomes of the parent plant. **Driesch** raised complete embryo from a part of egg or from isolated early blastomeres.
2. **Effect of Environment on Germ Cells through Somatic Cells:** **Heslop Harrison** demonstrated that a pale variety of moth, *Selonia bilunaria*, when fed on manganese coated food; a melanic variety of moth is produced. This breeds true to its colour showing permanent change in the genotype and phenotype of offspring. He also observed a melanic variety of this moth in area where food plants were infected with manganese salts from the industrial smoke. The influence of manganese is through somatic cells on to the germ cells.
3. **Direct Effect of environment on Germ Cell tower:** Tower exposed young ones of potato beetle to abnormal conditions of temperature and humidity. The heat treatment did not produce any somatic changes in the beetles themselves, but their offsprings showed marked colour changes in the next generation. These changes were passed on to the succeeding generations.

Muller demonstrated the role of X-rays in producing heritable variation in *Drosophila* by changes in the chromosome structure. C. Auerback in collaboration with Robinson and Carr produced heritable changes in *Drosophila* by using certain chemical mutagen like mustard gas. Thus, Neo-lamarckism proves that:

1. Germ cells are influenced by the environmental changes.
2. Germ cells may carry acquired or somatic variation to the offspring (Harrison's experiment).
3. Germ cells may be affected directly by the environmental factors (Tower's experiment).
4. Somatic characters are the result of interaction between genes and environment. It means environment does affect the gene expression.

Darwin's Theory of Natural Selection

Historical Aspect

In 1831, Darwin got an opportunity to travel on H.M.S. Beagle (a ship in which Charles Darwin sailed around the world) for a voyage of world exploration. The voyage lasted for five years (1831-1836). During that period Darwin explored the fauna and Flora of a number of continents and islands. Later Beagle was sailed to the Galapagos Islands. Galapagos Islands consist of 14 main islands and numerous smaller islands which lie on the equator about 960 Km off the West Coast of South America in the Pacific Ocean. These islands are volcanic in origin and are called "a living laboratory of evolution". Darwin visited these islands in 1835 and spent a month there. He observed great variations among the organisms that lived on these islands.

Darwin noticed giant tortoises, (Sp: *galapago*), metre-long marine and land iguanas, many unusual plants, insects, lizards, sea shells and birds on Galapagos Islands. These giant tortoises may weigh as much as 275 kg, grow to 183 cm in length and attain an age of 200 to 250 years. The Spanish word for tortoise, *galapago*, gives the islands their name. Birds of Galapagos Islands influenced Darwin to think about the evolutionary change. These birds were called finches. Finches were designated as Darwin's finches by Dr David Lack (1947).

Charles Robert Darwin returned to England in October 1836 from his 5-year expedition. In 1838 he came across with a book **An Essay on the Principles of Population** written by Thomas Robert Malthus, a British economist (1766-1834) and was published in 1799.

In 1798 T.R. Malthus, put forward a **theory of human population growth**. (i) He stated that population grows geometrically when unchecked; whereas the means of its subsistence like food grow only arithmetically. (ii) Naturally, after some time an imbalance would occur in the population and the environment. (iii) When the imbalance reaches a certain value, some factors like hunger, epidemics, floods, earthquakes, war,

etc. will bring the population to a desired level. Such a population "crash" is called **catastrophic control of population**. These factors were called "**Positive checks**" by Malthus. Darwin was influenced by Malthus's theory of human population growth.

Darwin noticed the conflict between resources of population and its continued reproductive pressure. Darwin considered that like in humans, competition exists among all living things. Thus Darwin was much influenced by Malthus Theory of human population growth. Darwin came to know that humans have been modifying wild plants and animals to suit their requirements. The breeders have successfully produced cows that give increased amount of milk. He also observed that humans have perfected the toy-like Shetland pony, the Great Dane dog, the sleek Arabian race horse and many cultivated crops and ornamental plants. Many crop plants like broccoli, cabbage, cauliflower, etc have also been produced through selective breeding.

While Darwin was busy in formulating his theory of natural selection, he received a brief essay from Alfred Wallace in June 1858. **Alfred Wallace** (1823-1913), a naturalist from Dutch East Indies was working on Malay Archipelago (present Indonesia). The essay was titled "**On the Tendencies of varieties to Depart Indefinitely from the original type**". The thinking of both Darwin and Wallace in respect of organic evolution was similar.

Finally in November 1859 Darwin published his observations and conclusion in the form of book. The full title of his book was ***On the origin of species by means of Natural Selection: The Preservation of Races in the Struggle for life***. Actually Darwin gave brief description of origin of species; however he described in detail how populations become well adapted to their environments through natural selection.

The Principle of Natural Selection

The principle of natural selection stems from five important observations and three inferences (Ernst Mayr 1982) which have been mentioned below.

Observation	Inferences
<ol style="list-style-type: none"> 1. All species have such great potential of fertility that their population size would increase exponentially if all the individuals that were born reproduce successfully. 2. Most populations are normally stable in size, except for seasonal fluctuations. 3. Natural resources are limited. 	

4. Individuals of a population vary extensively in their characteristics; no two individuals are exactly alike.
5. Much of this variation is stable.

- (a) Production of more individuals than the environment can support leads to a struggle for existence among the individuals of population, with only a fraction of offspring surviving each generation.
- (b) Survival in the struggle for existence is not random, but depends in part on the heredity constitution of the surviving individuals whose inherited characters fit them best in their environment are likely to leave more offspring than less fit individuals.
- (c) The unequal ability of individuals to survive and reproduce will lead to a gradual change in a population with favourable characteristics accumulating over the generations.

Natural selection is differential success in reproduction and its product is adaptation of organisms to their environment. Thus natural selection occurs through an interaction between the environment and the variability inherent in the population.

Salient Features of Darwin's Theory of Natural Selection

The main features of the theory of Natural Selection are as follows:

1. Over production (Rapid Multiplication). All organisms possess enormous fertility. They multiply in geometric ratio. Some examples are cited below:

Insects lay hundreds of eggs. A cod-fish lays several hundred eggs at a time. A female rabbit gives birth to six young ones in one litter and produces four litters in a year. Six month-old rabbit is capable of reproduction. If all the rabbits survived and multiplied at this rate, their number would be very large after some time. Each pair of mice produces dozens of young ones. It is assumed that elephant is the slowest breeder, which matures at the age of 30 years and lives for about 90 years. Each female gives rise to about six offspring. Thus some organisms (living beings) produce more offspring and others produce fewer offspring. This is called **differential reproduction**.

2. Limited Food and Space. Despite of rapid multiplication of all types of species, food and space and other resources remain limited. They are not liable to increase.

3. Struggle for Existence. The struggle for existence can be of three types.

(i) *Intraspecific Struggle.* It is the struggle between the individuals of the same species because their requirements like food, shelter, breeding places, etc. are similar. Many human wars are the examples of intraspecific struggle. *Cannibalism* (eating the individuals of its own species) is another example of this type of struggle.

(ii) *Interspecific Struggle.* It is the struggle between the members of different species. This struggle is normally for food and shelter. For example, a fox hunts out a rabbit, while the fox is preyed upon by a tiger.

(iii) *Environmental Struggle.* It is the struggle between the organisms and the environmental factors, such as drought, heavy rains, extreme heat or cold, earthquakes, diseases, etc. Thus, climate and other natural factors also help in restricting the number of individuals of particular species.

4. Appearance of Variations. Except the identical twins, no two individuals are similar and their requirements are also not exactly the same. It means there are differences among the individuals. These differences are called variations. Due to the variations some individuals would be better adjusted towards the surroundings than the others. Adaptive modifications are caused through the struggle for existence. *According to Darwin, the variations are gradual (continuous) and those which are helpful in the adaptations of an organism towards its surroundings would be passed on to the next generation, while the others disappear.*

5. Natural Selection or Survival of the Fittest. The organisms which are provided with favourable variations would survive, because they are the fittest to face their surroundings, while the unfits are destroyed. Originally it was an idea of **Herbert Spencer** (1820-1903) who used the phrase '*the survival of the fittest*' first time while Darwin named it as *natural selection*.

It is to be noted that only survival of the fittest is not enough. But organisms should also adapt or change themselves according to the changed conditions of the environment as environment is always changing. To explain the phenomenon of survival of the fittest, the extinct reptiles can be cited as an example. During the evolution of reptiles, giant reptiles, the dinosaurs, etc., appeared. Majority of them were herbivorous, but due to certain climatic changes, the vegetation disappeared and, therefore, most of them became extinct. However, small animals who could change their feeding habits from herbivorous to carnivorous diet survived, because they could easily get adapted to the changed environment. These, therefore, will survive more and hence are selected by nature. Darwin called it natural selection and implied it as a mechanism of evolution. Alfred Wallace a naturalist who worked in Malay Archipelago had also come to similar conclusions around the same time.

6. Inheritance of useful variations. The organisms after getting fitted to the surroundings transmit their useful variations to the next generation, while the non-useful variations are eliminated. Darwin could not differentiate between continuous and discontinuous variations. In this respect, Darwin agreed with Lamarck's views, because according to Darwin acquired characters which are useful to the possessor could be inherited.

7. Speciation (Formation of new species). Darwin considered that useful variations are transmitted to the offspring and appear more prominently in succeeding generations. After some generations these continuous and gradual variations in the possessor would be so distinct that they form a new species.

Weakness of Darwinism

Darwin was unable to explain the basis of variation and the mode of transmission of the variants to the next generation. In 1868, Darwin proposed the 'Theory of Pangenesis' to explain the mechanism of inheritance. According to this theory, every organ of the body produce minute hereditary particles, **pangenes or gemmules**, for example, heart gemmules from heart, liver gemmules from liver, leg gemmules from the leg and so on. He considered that the gemmules were carried through blood from every organ of the body and were collected into the gametes. However August Weismann's **Theory of Continuity of Germplasm** refuted the theory of Pangenesis.

Criticism of the Natural Selection Theory

(Objections against the Natural Selection Theory)

1. **Inheritance of Small Variations.** According to natural selection theory only useful variations are transmitted to the next generation, but sometimes small variations which are not useful for the possessor, are also inherited. It is beyond understanding that if the appearance of small wings in birds could help them in flying.
2. **Over-Specialization of Some Organs.** Some organs like tusks of elephants, antlers of deer have developed so much that instead of providing usefulness to the possessor, they often give hindrance to them. This theory cannot explain these facts.
3. **Vestigial Organs.** Why vestigial organs are present in some animals when they have no function? According to the Natural Selection Theory, vestigial organs should not be present.
4. **Arrival of the Fittest.** The theory only explains the survival of the fittest but, is unable to explain the arrival of the fittest.
5. **Degeneration of Organs.** The theory does not account for the degeneration of certain organs in animals.
6. **Discontinuous Variations.** The theory fails to explain the cause of sudden changes in the body. *The main drawback of Darwin's theory was lack of the*

knowledge of heredity and that is why he could not explain that how the variations are caused.

Darwin himself was conscious of the inadequacies of his theory, when he remarked that, "*I am convinced that natural selection has been the most important but not the exclusive means of modifications.*"

Evidences in Favour of Natural Selection

1. **Rate of Reproduction.** Rate of reproduction is many times higher than the rate of survival in all organisms.
2. **Limitation of Resources.** Food, space and other resources are limited.
3. **Struggle for Existence.** Competition or struggle for existence is seen in all organisms.
4. **Abundance of Variations.** Variations are so abundant in nature that no two individuals of a species are similar, not even the monozygotic twins (they possess some dissimilarities due to their environment).
5. **Production of New Varieties of Plants and Animals by Artificial Selection.** When man can produce various new varieties of plants and animals in a short period, nature with its vast resources and long time at its disposal can easily produce new species by selection.
6. **Mimicry and Protective Colouration.** They are found in certain animals and are products of natural selection.
7. **Correlation between Nectaries of Flowers and Proboscis of Insects (Entomophily).** The position of nectary in a flower and the length of proboscis in pollinating insects are wonderfully correlated.
8. **Pedigrees of Some Animals.** Pedigrees of horses, camels and elephants also support the Natural Selection Theory.

The mutation theory of evolution

Hugo DeVries based on his extensive studies on the 8 varieties of Evening Primrose, *Oenothera lamarckiana* noted that new characters originated by sudden changes in the wild type and were heritable. The plants with new characteristics transmitted these characteristics to their progeny. Each of the form was called *mutant* by DeVries and the new characteristics were called '*mutations*'. The theory formulated on the study of these forms was named '*Mutation Theory of Evolution*' which established that "*New species originate as a result of these large, discontinuous variations which appear suddenly and full-fledged and form the new species at once.*"

The main features of Mutation Theory are as follows:

- Mutations arise from time to time amongst the individuals of a naturally breeding population or species. The individuals with mutations are known as mutants. These mutants are markedly distinct from their parents.

- Mutations are large and sudden and are very different from fluctuating variations of Darwin, which are small and directional.
- Mutations may occur in any direction.
- Mutations are heritable.
- Mutations establish new forms, races, or species. Mutations are the primary forces behind speciation.
- Mutations are subjected to natural selection.
- Mutants found unsuitable are likely to be destroyed by natural selection.
- Since mutations appear full-fledged, there is no question of the significance of incipient stages in the development of an organ.

Critical evaluation of the Mutation Theory of evolution

- DeVries work was exposed to severe criticism soon after proposal. Darwinists contended that evolution resulted from gradual fluctuating inheritable differences over a long series of generations, whereas mutation is involved in sudden appearance of species differences.
- Extensive cytological studies showed that mutants of *Oenothera* are mostly polyploids rather than gene mutants. Later, Blakeslee working on *Datura* and T. H. Morgan on *Drosophila* showed that origin of species as described by DeVries in *Oenothera* is by no means exceptional but is a common thing among plants.
- Morgan (1909) showed that mutations are of all magnitudes in *Drosophila*. Today mutations are observed among bacteria, bacteriophages and viruses as well as in man and other living organisms. With increased knowledge of mutations it has become clear that mutations alone cannot account for evolution, but these furnish the raw material on which other forces can act to bring about the evolutionary change.

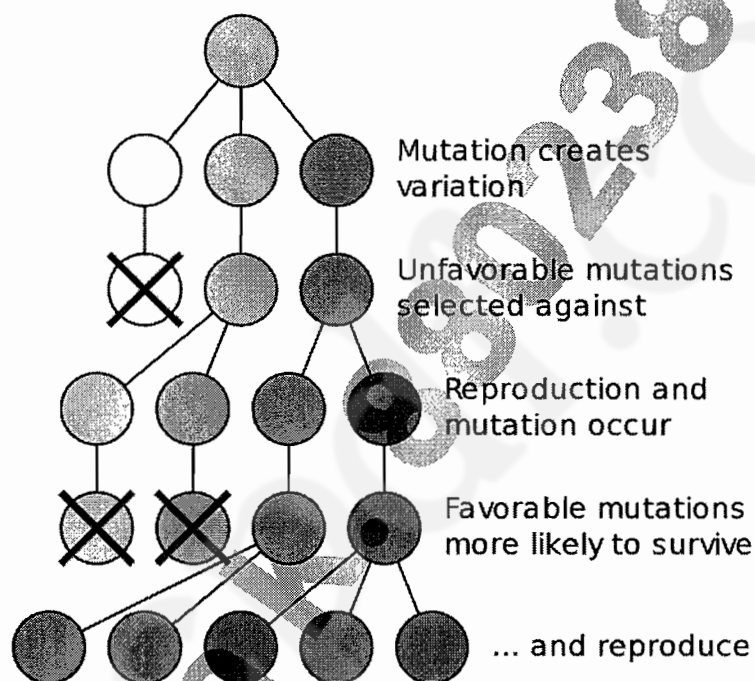
Modern concept of evolution

The **modern evolutionary synthesis** is a union of ideas from several biological specialties. This synthesis has been generally accepted by most working biologists. The synthesis showed that Mendelian genetics was consistent with natural selection and gradual evolution. The synthesis is still, to a large extent, the current paradigm in evolutionary biology.

Julian Huxley invented the term, when he produced his book, *Evolution: The Modern Synthesis* (1942). Other major figures in the modern synthesis include R. A. Fisher, Theodosius Dobzhansky, J.B.S. Haldane, Sewall Wright, E.B. Ford, Ernst Mayr, Bernhard Rensch, Sergei Chetverikov, George Gaylord Simpson, and G. Ledyard Stebbins.

Discoveries of early geneticists were difficult to reconcile with gradual evolution and the mechanism of natural selection. The synthesis reconciled the two schools of thought, while providing evidence that studies of populations in the field were crucial to evolutionary theory. It drew together ideas from several branches of biology that had become separated, particularly genetics, cytology, systematics, botany, morphology, ecology and paleontology.

Modern evolutionary synthesis is also referred to as the **new synthesis**, the **modern synthesis**, and the **evolutionary synthesis**. The essential proposition of the modern synthesis is summarised below.



Speciation

The millions of species now inhabiting this planet have evolved from a common ancestor, and the multiplication in the number of species has been generated as single species have split into two.

What is Speciation?

Species is a Latin word meaning “kind” or “appearance.” The primary definition of species used most frequently in evolutionary analysis was proposed by biologist **Ernst Mayr**. Mayr (1963) gave the **biological species concept** which defines species in terms of interbreeding. This biological species concept defines a species as a population or group of populations whose members have the potential to interbreed in nature and

produce viable, fertile offspring, but are unable to produce viable, fertile offspring with members of other populations. In other words, the members of a biological species are united by being reproductively compatible and at the same time they are reproductively isolated from the members of other species.

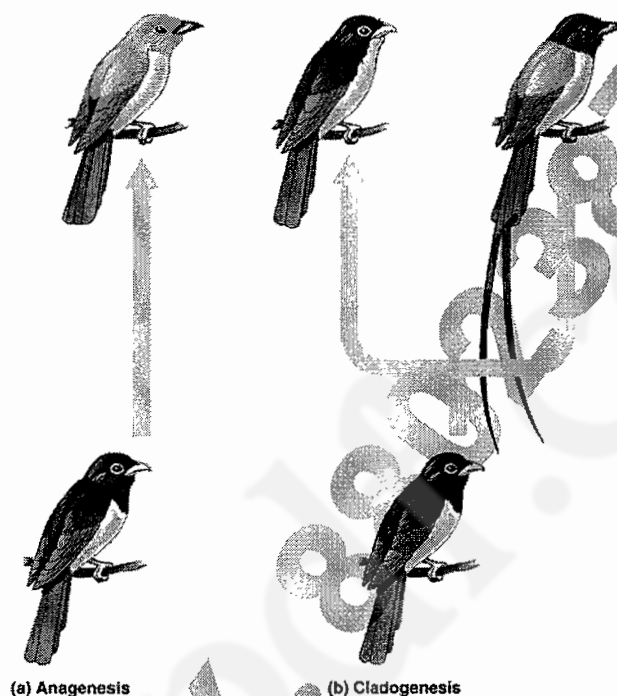


Figure 9: The two patterns of speciation

Speciation refers to the evolutionary process by which new biological species arise. Speciation is one of the most significant evolutionary processes because the appearance of new species is the ultimate source of biological diversity.

It is now universally accepted that new species arise from pre-existing species, rather than arising *de novo*, as earlier speculated.

The Patterns of Speciation

There are two basic patterns of speciation: **anagenesis** and **cladogenesis**.

1. **Anagenesis** is also called phyletic evolution. It is the accumulation of changes which gradually transform a given species into a species with different characteristics.
2. **Cladogenesis** (from the Greek klados, branch) is also called branching evolution. It is the splitting of a gene pool into two or more separate pools, which each give rise to one or more new species. Only cladogenesis promotes biological diversity by increasing the number of species.

The Process of Speciation

Speciation has mostly occurred when two populations have evolved independently (in the same, adjacent or separate habitat(s), and accumulated incompatible genetic differences. These incompatible genetic differences lead to reproductive isolation.

When do we say that speciation has occurred?

According to the Biological Species Concept: "*species are groups of interbreeding natural populations that are reproductively isolated from other such groups.*" The expression "reproductively isolated" means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding.

Based on the above concept, we can say that *speciation occurs (i.e. new species arise) when two populations, earlier belonging to the same species, become reproductively incompatible (i.e. reproductively isolated) due to accumulated genetic differences.*

As recognized by Dobzhansky (1970), reproductive isolation can manifest in one or more of the following ways.

1. Premating or prezygotic mechanisms prevent the formation of hybrid zygotes

- i. **Ecological or habitat isolation.** The populations concerned occur in different habitats in the same general region, e.g. European mosquito, *Anopheles labranchiae*, is found in brackish water, while *A. maculipennis* is found in running freshwater.
- ii. **Seasonal or temporal isolation.** Mating or flowerings times occur at different seasons, e.g. *Pinus radiata* and *P. muricata* are found in close proximity in California but shed their pollen at different times.
- iii. **Sexual or behavioural isolation.** Mutual attraction between the sexes of different species is weak or absent, e.g. in the European bush cricket, *Ephippiger*, females show a strong preference for the chirp pattern of the courtship song produced by males of the same species.
- iv. **Mechanical isolation.** Physical non-correspondence of the genitalia or the flower parts prevents copulation or the transfer of pollen, e.g. some damselflies have very complex genitalia preventing inter-mating.
- v. **Isolation by different pollinators.** In flowering plants, related species may be specialized to attract different pollinators, e.g. male bees pollinate bee orchids by 'copulating' with bee-mimicking flowers. Different species of bee orchid mimic different bee species making cross-fertilization impossible.

- vi. **Gametic isolation.** In organisms with external fertilization, female and male gametes may not be attracted to each other. In organisms with internal fertilization, the gametes or embryos of one species may be unviable in the physical environment of other species.

2. Postmating or zygotic isolating mechanisms reduce the viability or fertility of hybrid zygotes

- Hybrid inviability.** Hybrid zygotes have reduced viability or are inviable. In the north American crickets, matings between *Gryllus pennsylvanicus* males and *G. firmus* females fail to produce any offspring.
- Hybrid sterility.** The F₁ hybrids of one sex or of both sexes fail to produce functional gametes.
- Hybrid breakdown.** The F₁-hybrids are normal, healthy, and fertile, but the F₂-generation contains many weak or sterile individuals.

The models of speciation

As mentioned earlier, speciation has mostly occurred when two populations have evolved independently (in the same, adjacent or separate habitat/s), and accumulated incompatible genetic differences. These incompatible genetic differences lead to reproductive isolation (Figure 2).

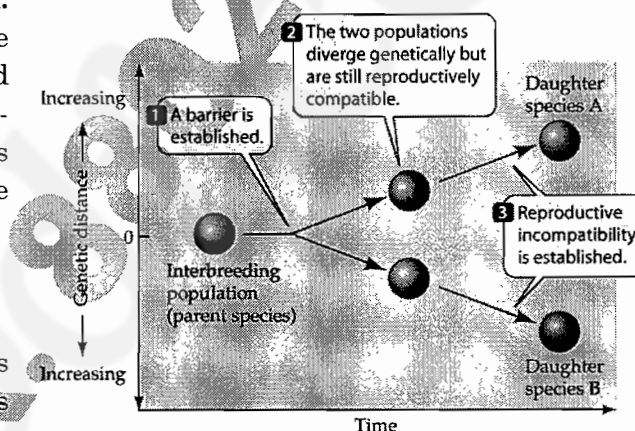
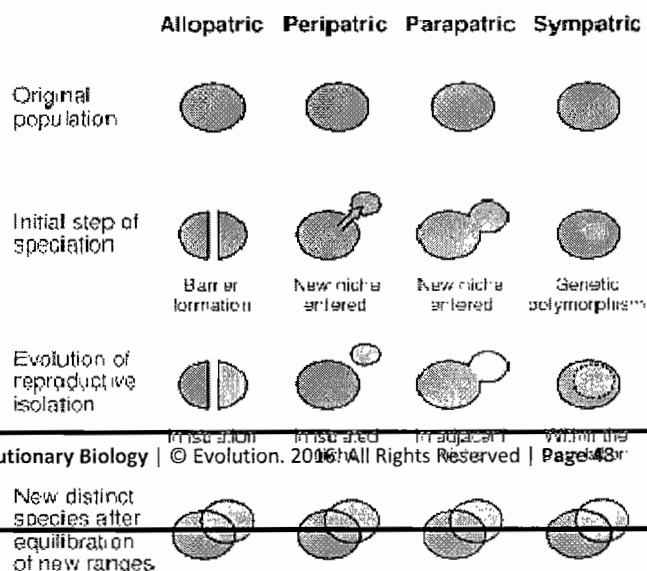


Figure 2: Speciation occurs by accumulated incompatible genetic differences

There are four modes of natural speciation, based on the extent to which speciating populations are geographically isolated from one another:

1. allopatric
2. peripatric
3. parapatric
4. sympatric

The figure below summarizes that in different models of natural speciation there are different patterns of geographical isolation



to which the members of speciating populations are subjected.

Allopatric Speciation

During allopatric speciation, a population splits into two geographically isolated allopatric populations (for example, by habitat fragmentation). Over a period of time, the isolated populations may undergo genotypic divergence (and in many cases, phenotypic divergence also) as they:

- (a) sustain different types of mutation
- (b) become subjected to dissimilar selective pressures
- (c) independently undergo genetic drift.

When the populations come back into contact, they have evolved such that they are reproductively isolated and are no longer capable of exchanging genes.

Observed instances include speciation in Darwin's Galápagos Finches and speciation of the gymnosperm tree *Cycas* during the Mesozoic.

Peripatric Speciation

Peripatric speciation was originally proposed by Ernst Mayr. Peripatric speciation is a form of speciation where new species are formed in isolated peripheral populations. This is similar to allopatric speciation in the sense that populations are isolated and prevented from exchanging genes. However, in peripatric speciation, one of the populations is much smaller than the other.

Peripatric speciation is related to the concept of a Founder effect, because small living populations may undergo selection bottlenecks.

AR Templeton (1980) in his paper titled "The theory of speciation via the founder principle" proposed that Genetic drift plays a significant role in peripatric speciation. This proposal is logical because the effects of genetic drifts are very pronounced in smaller populations, as it happens in peripatric speciation.

Observed instances of peripatric speciation include:

- Mayr's bird fauna
- The Australian bird *Petroica multicolor*
- Reproductive isolation occurs in populations of *Drosophila* subject to population bottlenecks

Parapatric Speciation

In parapatric speciation, the zones of two diverging populations within a large geographical area are separate but do overlap. There is only partial separation afforded by geography, so individuals of each species may come in contact or cross the barrier

from time to time, but reduced fitness of the heterozygote leads to selection for behaviours or mechanisms which prevent breeding between the two species. So, in parapatric speciation, the population is continuous, but nonetheless, the population does not mate randomly.

In this type of speciation, the evolution of reproductive isolating mechanisms occurs when a population enters a new niche or habitat *within the range of the parent species*. Generally, this occurs when there has been a drastic change to the environment within the original species' habitat.

A good example is the grass *Anthoxanthum*, which has undergone parapatric speciation after mine contamination of its habitat area. Selection for resistance/tolerance to certain metals has occurred. Flowering time generally changed (a strong selection against interbreeding—as the hybrids are generally ill-suited to the environment) and often plants will become self-pollinating.

All the instances of ring species are believed to be the outcome of parapatric speciation. Such as:

- The *Larus* gulls form a ring species around the North Pole.
- The *Ensatina* salamanders, which form a ring round the Central Valley in California.
- The Greenish Warbler (*Phylloscopus trochiloides*), around the Himalayas.

Sympatric Speciation

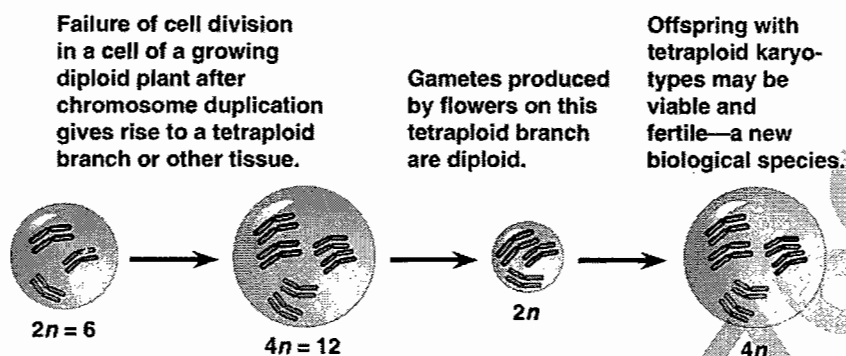
In sympatric speciation, species diverge while inhabiting the same place (sympatric). Mechanisms of sympatric speciation include **chromosomal changes** and **nonrandom mating** that reduces gene flow.

Chromosomal changes in sympatric speciation

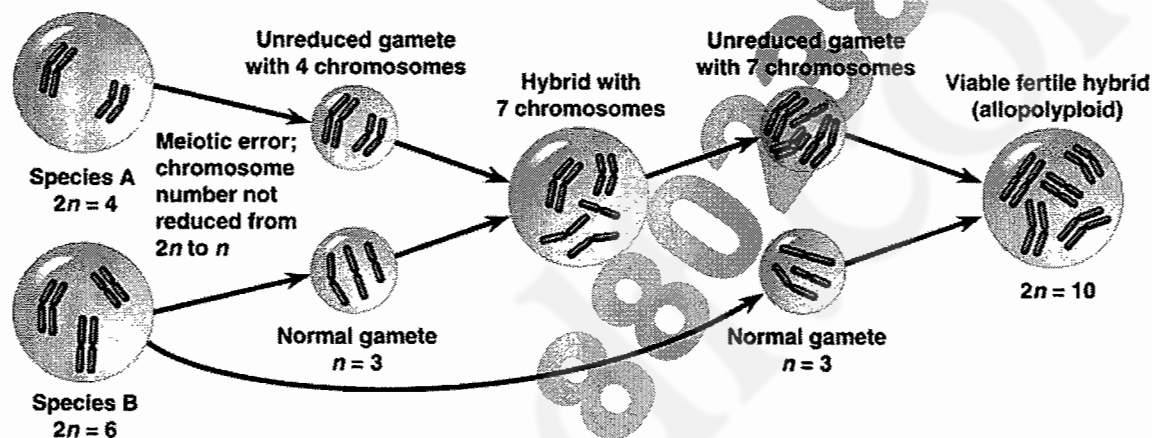
Increased ploidy levels, i.e. Polyploidy, is a mechanism often attributed to causing some speciation events in sympatry. **Many types of polyploidy, especially allopolyploidy lead to instant speciation.** This is also called **Quantum Speciation** or **Saltation**. It overlaps in scope with **Stasipatric Speciation** too, which is described as speciation by chromosomal rearrangements.

It should be noted that not all polyploids are completely reproductively isolated from their parental plants, so an increase in chromosome number may not always result in speciation.

The following figure shows how autopolyploidy leads to instant speciation.



The role of allopolyploidy in speciation is shown in the figure below.



Known instances:

The origin of new polyploid plant species is common enough and rapid enough that scientists have documented several such speciations. For example, two new species of goatsbeard plants (genus *Tragopogon*) originated in the Pacific Northwest in the mid-1900s. These species, *T. dubius*, *T. pratensis*, and *T. porrifolius*, are now common weeds in urban wastelands.

Many important agricultural crops—such as oats, cotton, potatoes, tobacco, and wheat—are polyploids. The wheat used for bread, *Triticum aestivum*, is an allohexaploid (six sets of chromosomes, two sets from each of three different species). The first of the polyploidy events that eventually led to modern wheat probably occurred about 8,000 years ago in the Middle East as a spontaneous hybrid of an early cultivated wheat and a wild grass.

Polyploid speciation also occurs in animals (*Xenopus laevis*), although it is less common than in plants.

Nonrandom mating in sympatric speciation

Other mechanisms than polyploidy can also lead to sympatric speciation in both animals and plants. For example, reproductive isolation can occur when a subpopulation is able to exploit a resource not used by the parent population.

Such is the case with the North American apple maggot fly, *Rhagoletis pomonella*. The fly's original habitat was native hawthorn trees, but about 200 years ago, some populations colonized apple trees introduced by European settlers. Apples mature more quickly than hawthorn fruit, and so the apple-feeding flies have been selected for rapid development. These apple-feeding populations now show temporal isolation from the hawthorn-feeding *R. pomonella*. Although the two groups are still classified as subspecies rather than separate species, speciation appears to be well under way.

A case study of sympatric speciation: In Lake Victoria in eastern Africa, the subdivision of many original fish populations into groups adapted to exploiting different food sources has been a major factor contributing to this rapid speciation. One such example is Cichlid fishes, where *Pundamilia nyererei* and *P. pundamilia* are related species that differ in color. *P. nyererei* is red and *P. pundamilia* is blue. Seehausen & Van Alphen (1998) performed a laboratory experiment on the mating preferences of the two species. They first tested the preferences of females of both species for males of one species or the other, in normal light. The result was that the females of both species preferred conspecific males. The two species show prezygotic isolation by mating behavior. Seehausen and van Alphen then repeated the experiment, but in monochromatic light, in which the color difference between the two species was invisible. Now the females of both species show no preference between red and blue males. The experiment shows that the prezygotic isolation is due to the color patterns of the two fish species. In such cases, no post zygotic barriers have developed. This is a controversial case, where the completeness of speciation is debatable.

Artificial Speciation

New species have been created by domesticated animal husbandry and plant breeding.

For example, domestic sheep were created by hybridisation, and no longer produce viable offspring with *Ovis orientalis*, one species from which they are descended. On the other hand, plant geneticists create new polyploids in the laboratory by using chemicals that induce meiotic and mitotic errors. By harnessing the evolutionary process, researchers can produce new hybrid species with desired qualities, such as a hybrid combining the high yield of wheat with the hardiness of rye.

Role of Reinforcement in Speciation

Reinforcement is the process by which natural selection increases reproductive isolation. Reinforcement can occur as follows.

When two populations previously kept apart come back into contact, the reproductive isolation between them might be complete or incomplete. If it is complete, speciation has occurred. If it is incomplete, hybrids would be produced. If the hybrids had lower fitness than either parental form, selection would act to increase the reproductive isolation.

Reinforcement is a necessary requirement for both the parapatric and sympatric theories of speciation. It is the process by which a hybrid zone (an area of contact between different forms of a species) develops into a full species barrier.

Reinforcement is known as **secondary reinforcement** if the reproductive isolation has partly evolved allopatrically, and is then reinforced when the two populations come into secondary contact.

2. Origin of life

What is life?

In Biology, *Life* is defined as *that state of being when an entity can carry out self sustaining activities on its own, respond to the environmental changes and reproduce itself.*

NASA (The National Aeronautics and Space Administration of the USA) defines life as *a self-sustained, self reproducing chemical system capable of undergoing Darwinian evolution.*

Living entities possess extra-ordinary attributes which distinguish them from other collections of matter.

1. A high degree of chemical complexity and microscopic organization
2. Systems for extracting, transforming and using energy from the environment
3. A capacity for precise self-replication and self-assembly
4. Defined functions for each of their components and regulated interactions among them
5. Mechanisms for sensing and responding to environmental changes
6. A history of evolutionary changes

What is meant by origin of life?

The Earth formed about 4.57 billion years ago, while the earliest fossils of cellular forms available today correspond to a period about 3.5 billion years ago. So the current view is that the first living form, i.e. the earliest cell, arose from the non-living materials of the early earth about 3.8 – 3.6 bya (billion years ago).

Origin of life means the earliest advent of *a self-sustained, self reproducing chemical system capable of undergoing Darwinian evolution* on the earth. Currently, the widely accepted estimates suggest that such a system emerged for the first time on the earth *about 3.8 billion years ago by chemical abiogenesis.*

There are so many fundamental similarities among all the living forms (in cellular-molecular organization, biochemical pathways, genes & gene expression, molecular genetic pathways etc.) that the biologists today conclude that *origin of life occurred only once on the earth and all the living forms today or in the past have ultimately descended from a single common universal ancestor.*

How did the life originate?

Various theories

The question of origin of life has intrigued the mankind deeply since ancient times. Hence it is logical that a large number of explanations have been proposed from time to time by various workers.

Even today, the origin of life is an important field of research due to its profound impact on biology and human understanding of the natural world.

The Process according to the currently accepted models

The currently accepted explanations on the origin of life are based on **Biochemical Abiogenesis**. Abiogenesis means the generation of life from non-living matter.

Biochemical Abiogenesis proposes that life has arisen on the earth by a route of gradually increasing biochemical complexity and sophistication using the simplest of the molecules present in the early environment of the earth.

This concept is different from the Classical Abiogenesis or *Aristotelian Abiogenesis* (also known as *Spontaneous Generation Model*) – the theory according to which fully formed, complex living organisms sometimes arise suddenly from not-living matter. We know today that it does not occur.

Important proposals & evidences in the Biochemical Abiogenesis Model

1. In 1924, Alexander Ivanovich Oparin proposed that simple one-celled life forms might have come from the simple organic molecules present in the early earth's atmosphere. From geological evidences, he proposed theoretical conditions for the early earth. The early atmosphere was quite different from the modern atmosphere and probably resembled atmospheres of other planets.

In the early atmosphere the following chemicals abounded but there was no free oxygen gas.

1. Hydrogen
2. Ammonia
3. Methane
4. Carbon Dioxide
5. Water
6. Nitrogen

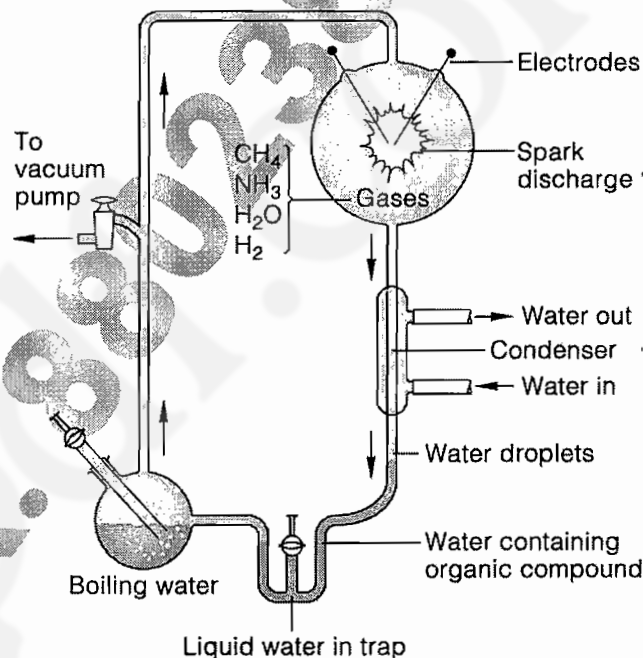
Oparin proposed that in the extreme primitive conditions it was possible that these simple molecules combined with one another to give rise to the bio-organic macromolecules. Later, these bio-organic macromolecules might have combined in a self-replicating system and gave rise to the earliest cells.

2. In 1928, English biochemist J.B.S. Haldane proposed that life might have arisen on the earth when Oparin's early atmosphere was subjected to energy inputs in the forms of Heat from the cooling earth and Ultraviolet radiation. Haldane also said that lightening might have provided the sudden but large inputs of additional energy for attaining biochemical complexity.

3. In 1953, Stanley Miller, a graduate student in biochemistry, built the apparatus shown here. He filled it with

1. methane (CH_4)
 2. ammonia (NH_3)
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 4. hydrogen (H_2)
- But no oxygen

He hypothesized that this mixture resembled the atmosphere of the early earth. The mixture was kept circulating by continuously boiling and then condensing the water. The gases passed through a chamber containing two electrodes with a spark passing between them. At the end of a week, Miller used paper chromatography to show that the flask now contained several amino acids, purines, pyrimidines as well as some other organic molecules.



This experiment was the validation of the earlier two theories.

In the years since Miller's work, many variants of his procedure have been tried. Virtually all the small molecules that are associated with life have been formed including:

1. 17 of the 20 amino acids used in protein synthesis, and
2. all the purines and pyrimidines used in nucleic acid synthesis.

Yet, there are *three* serious limitations to this experimental validation:

1. Abiotic synthesis of ribose — and thus of nucleosides — has been much more difficult.

2. Supramolecular Polymerisation of biomolecules could not be attained in such experiments. Without this, complex cellular molecules and structures cannot form.
3. Recently available evidences from geology have suggested that the gases Miller used (a reactive mixture of methane and ammonia) in his reaction did not exist in large amounts on early Earth. These evidences indicate that the primeval atmosphere contained an inert mix of carbon dioxide and nitrogen.

When Miller repeated his experiment using the correct combination of gases (CO_2 , N_3 , H_2O , and H_2) in 1983, the complex organic mixture obtained in the earlier experiment did not form. Instead, the mix created a thin solution containing only a few amino acids. It was also discovered later that these reactions were also producing nitrites. The Nitrites were turning the water acidic—which prevents amino acids from forming further.

These limitations have been explained by subsequent theories and experimental findings.

4. In March 2007, Jeffrey Bada (from Scripps Institution of Oceanography in La Jolla, California) worked out that primitive Earth also contained iron and carbonate minerals which neutralized nitrites and acids. This neutralization allowed amino acids to form. When Bada repeated the Miller's experiment of 1983 with CO_2 , N_3 , H_2O , and H_2 along with added iron and carbonate minerals, he could obtain a mixture full of amino acids and some purines.

5. A possible answer to this polymerization problem was provided in 1980s by Günter Wächtershäuser, in iron-sulfur world theory. In this theory, he postulated the evolution of (bio) chemical pathways independent on external sources of energy (e. g. simulated lightning or UV irradiation). "Wächtershäuser systems" come with a built-in source of energy, sulfides of iron and other metals (e. g. pyrite). The energy released from redox reactions of these metal sulfides is not only available for the synthesis of organic molecules, but also for the formation of oligomers and polymers. Therefore, such systems may be able to evolve to autocatalytic sets of self-replicating, metabolically active entities.

Even though the problem of energy input for polymerization was resolved, there still was an important missing link. That was – *What were the catalysts in early biomolecular polymerizations?* This was a valid question, because no biomolecular polymerization as we know today occurs without catalysis.

This question was answered by the theory given below.

6. **Clay theory of the origin of life:** A hypothesis for the origin of life based on clay was given by Dr A. Graham Cairns-Smith of Glasgow University in 1985. It postulates that the complex organic molecules arose gradually on a non-organic replication platform made of silicate crystals. Cairns-Smith argued that silicate crystals in

combination to Nickel – Iron (as found in Clay) provided an efficient catalytic system for chemical conjugation and polymerization.

7. The Earliest Self Replicating Biomolecules and PNA / RNA World formation:

When the structure of DNA was described by Watson and Crick in 1953, it was proposed that DNA was the first dominant biomolecule during the early steps towards the origin of life. The basis of this argument was that DNA has a self-complementary double stranded structure which allowed it to replicate. Before this proposal, the proteins were believed to be the earliest dominant biomolecules due to their versatile functional nature.

However, both the molecules speculated to be the early dominant molecules had certain limitations. First of all, DNA – despite a self-complementary double stranded structure – cannot replicate without the catalytic assistance of a number of proteins. Similarly, the limitation with proteins is that they are constructed by linking amino acids under the genetic instruction of DNA.

Thus, it was obvious that neither DNA nor Proteins could be the earliest class of dominant biomolecules.

In mid-1980, Sidney Altman and Thomas Cech separately published their discovery of self-splicing (catalytic) RNA. Thus, finally a class of biomolecule was identified which could store genetic information as well as could carry out catalytic functions. In 1986, Walter Gilbert coined the term **RNA World** to describe a time during which RNA was the primary information and catalytic molecule.

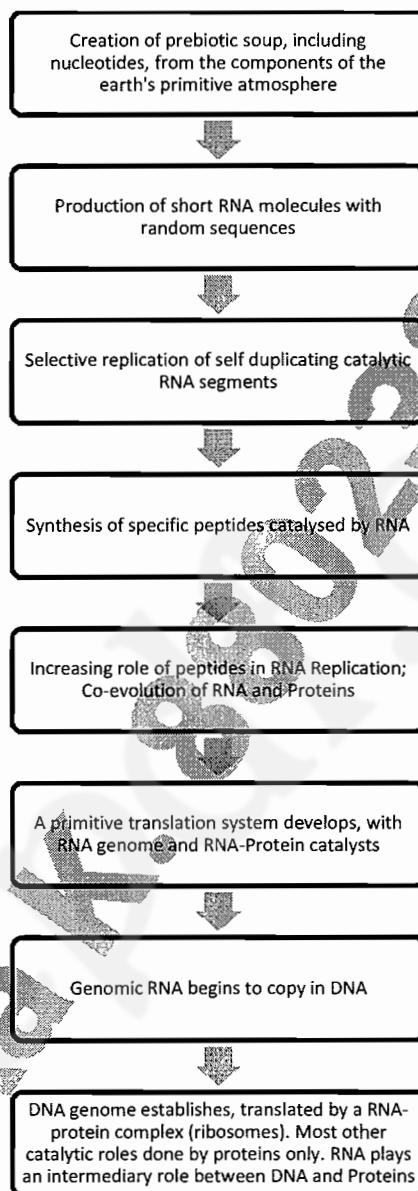
The RNA world hypothesis suggests that short RNA molecules could have spontaneously formed that would then catalyze their own continuing replication.

A proposed alternative to the RNA World is called PNA World, dominated by peptide nucleic acids. PNA is more stable than RNA and appears to be more readily synthesised in prebiotic conditions, where especially the synthesis of ribose and adding phosphate groups are problematic.

The transition between the PNA world and the RNA world probably occurred as the conditions on the earth began to be more benign. The plausibility of this scheme is supported by laboratory experiments showing that PNA can act as a template for the synthesis of complementary RNA molecules.

In any self replicating system, Darwinian natural selection is bound to operate. In a mature RNA world, different forms of RNA competed with each other for free nucleotides, and were subjected to natural selection. The most efficient molecules of RNA, the ones able to catalyze their own reproduction, survived and finally gave rise to the modern RNA. It is possible that competition between RNA favored the emergence of cooperation between RNA molecules opening the way to more complex supra molecular

assemblies. DNA, Proteins and other biomolecules were recruited later into life. The possible sequence of events is shown below in the process chart.



8. The transition from organic molecules to protocells: The question as to how organic molecules formed a protocell remains largely unanswered. However, there are many different hypotheses regarding the path that might have been taken from simple organic molecules to protocells, cells, and metabolism. According to the leading proposals, the transition from organic molecules to the protocells (which took about half a billion years) can be summarized through the following landmarks:

Formation of Prebionts

Prebionts were the nonliving suprabiomolecular structures that evolved later into the first living cells.

Formations of Coacervates

- Coacervates are organic molecules surrounded by a film of water molecules
- They selectively absorb materials from surrounding water and incorporate them into their structure
- The coacervates were not random arrangement of molecules but represented well organized and self replicating systems

Formation of Protobionts

Protobionts are organic molecules surrounded by a double membrane.

The protobionts with a well organized energy capture, transformation and utilization mechanism plus self replicative abilities were the earliest cells, thus accomplishing the origin of life for the first and final time on the earth.

It is generally accepted that all the subsequent living forms on the earth arose from this universal ancestor. The possible events were:

1. Growing functional and structural specialization in the earliest cells
2. Emergence of eukaryotic cells by endosymbiosis
3. Early divergence of the eukaryotes
4. Emergence of multicellular forms
5. Growing diversity due to speciation

A new approach: Metabolism First

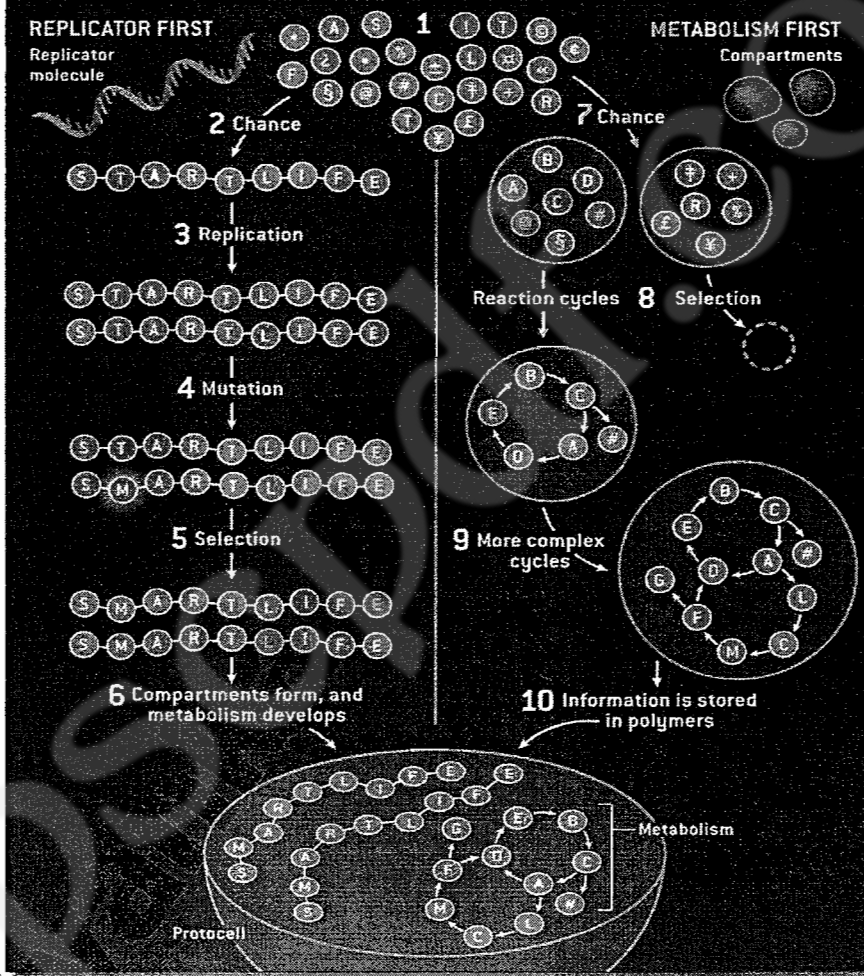
Recently, a new approach to resolve the question on the origin of life has also emerged. It has been reviewed in June 2007 issue of *Scientific American* by Robert Shapiro of New York University. While the early postulates emphasize on the early appearance of nucleic acids ("genes-first" or "replicator first"), the newer approach stresses on the evolution of biochemical reactions first "metabolism-first". It argues that without a definite metabolism and a source of bioenergy, the replicator system cannot arise. This proposal is diagrammatically summarized below.

REPLICATOR VS. METABOLISM

Scientific theories of the origin of life largely fall into two rival camps: replicator first and metabolism first. Both models must start from molecules formed by nonbiological chemical processes, represented here by balls labeled with symbols [1].

In the replicator-first model, some of these compounds join together in a chain, by chance forming a molecule—perhaps some kind of RNA—capable of reproducing itself [2]. The molecule makes many copies of itself [3], sometimes forming mutant versions that are also capable of replicating [4]. Mutant replicators that are better adapted to the conditions supplant earlier versions [5]. Eventually this evolutionary process must lead to the development of compartments (like cells) and metabolism, in which smaller molecules use energy to perform useful processes [6].

Metabolism first starts off with the spontaneous formation of compartments [7]. Some compartments contain mixtures of the starting compounds that undergo cycles of reactions [8], which over time become more complicated [9]. Finally, the system must make the leap to storing information in polymers [10].



3. Role of RNA in origin and evolution of life

Origin of life

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Biochemical Abiogenesis Model

Biochemical abiogenesis model explains how biological life arose from inorganic matter through natural processes of increasing chemical complexity. Abiogenesis occurred between 3.9 and 3.5 billion years ago.

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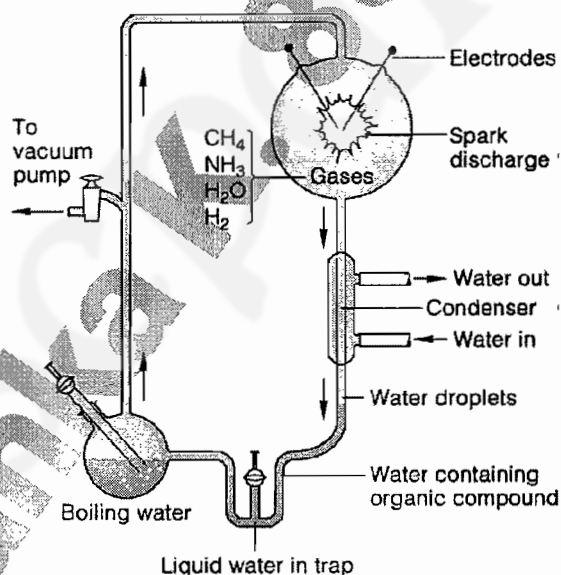


Figure 10: Miller's Experiment

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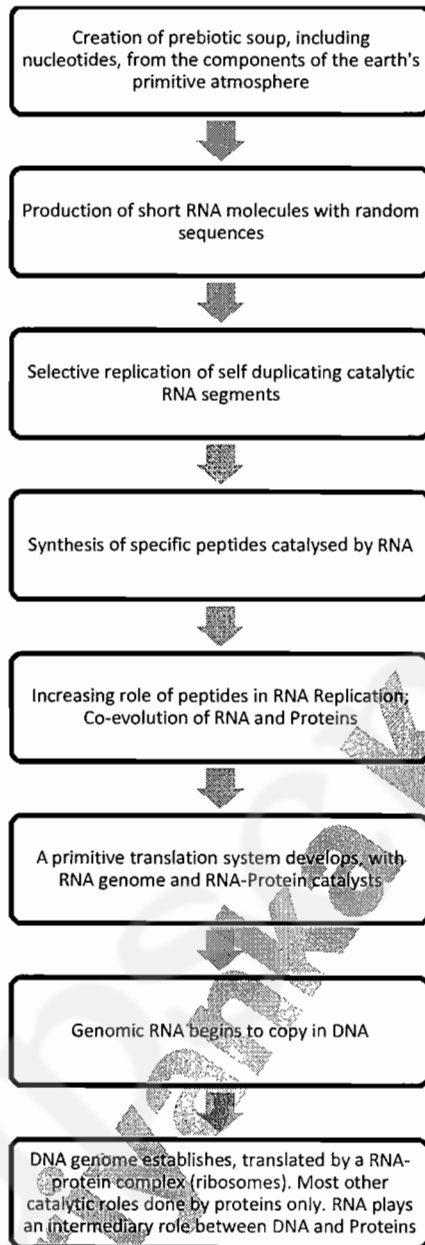
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Support for the RNA world model

An *RNA world* existed on Earth before modern cells arose. According to this hypothesis, RNA stored both genetic information and catalyzed the chemical reactions in primitive

cells. Only later in evolutionary time, DNA took over as the genetic material and proteins become the major catalyst and structural component of cells.

The **RNA world hypothesis** proposes that RNA was, before the emergence of the first cell, the dominant, and probably the only, form of life on Earth.

This hypothesis is supported by RNA's multiple abilities.

- To participate in the storage, transmission, and duplication of genetic information (similarly to DNA)
- To act as a ribozyme (similar to an enzyme), catalyzing certain reactions.

Thus, from the point of view of reproduction, molecules exist for two basic purposes: self-replication and catalysis assisting self-replication. DNA is capable of self-replication, but only assisted by proteins. Proteins are excellent catalysts, but fail to catalyze processes complex enough to recreate themselves, individually. RNA is capable of both catalysis and self-replication, which is the biggest support for the RNA World Hypothesis.

In 2001, the RNA world hypothesis was given a major boost with the deciphering of the 3-dimensional structure of the ribosome, which revealed that the key catalytic sites of the ribosome were composed of RNA, with proteins playing only a structural role in holding the ribosomal RNA together. Specifically, the formation of the peptide bond, the reaction that binds amino acids together into proteins, is catalyzed solely by RNA. This finding suggests that RNA molecules were responsible for (or at the very least capable of) generating the first proteins.

Other abilities of RNA also support the model. They include:

- To undergo allosteric conformational changes, either in response to small molecules or to other RNAs
- To fold up in many various ways and perform various tasks. Even today RNA plays a number of intermediary role between DNA and Proteins:
 1. Primer formation for DNA replication
 2. Telomere replication by Telomerase activity
 3. Transcription
 4. Splicing and Alternate splicing
 5. mRNA editing by Guide RNA system
 6. Heterochromatization of X chromosome [XIST]
 7. Translation [Peptidyl Transferase Centre]
 8. Riboswitches to regulate Transcription and Translation
 9. RNAi
 10. 7SL RNA in Protein Targeting to the RER lumen for core glycosylation
- Many of the cofactors that play so many roles in life are based on ribose; for example:
 1. ATP
 2. NAD
 3. FAD

4. coenzyme A
5. cyclic AMP
6. GTP

Conclusion

From our knowledge of present-day organisms and the molecules they contain, it seems likely that the development of the directly autocatalytic mechanisms fundamental to living systems began with the evolution of families of molecules that could catalyze their own replication. With time, a family of cooperating RNA catalysts probably developed the ability to direct synthesis of polypeptides. DNA is likely to have been a late addition: as the accumulation of additional protein catalysts allowed more efficient and complex cells to evolve, the DNA double helix replaced RNA as a more stable molecule for storing the increased amounts of genetic information required by such cells.

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